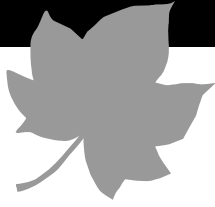


ORIGINAL
ARTICLE



A 40,000-year woodrat-midden record of vegetational and biogeographical dynamics in north-eastern Utah, USA

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ABSTRACT

Aim A conspicuous climatic and biogeographical transition occurs at 40–45° N in western North America. This pivot point marks a north–south opposition of wet and dry conditions at interannual and decadal time-scales, as well as the northern and southern limits of many dominant western plant species. Palaeoecologists have yet to focus on past climatic and biotic shifts along this transition, in part because it requires comparisons across dissimilar records [i.e. pollen from lacustrine sediments to the north and plant macrofossils from woodrat (*Neotoma*) middens to the south]. To overcome these limitations, we are extending the woodrat-midden record northward into the lowlands of the central Rocky Mountains.

Location Woodrat middens were collected from crevices and rock shelters on south-facing slopes of Dutch John Mountain (2000–2200 m, 40°57' N, 109°25' W), situated on the eastern flanks of the Uinta Mountains in north-eastern Utah. The site is near the regional limits for *Pinus ponderosa*, *P. edulis*, *P. contorta*, *Cercocarpus ledifolius* var. *intricatus*, *Abies concolor*, *Ephedra viridis* and other important western species.

Methods We analysed pollen and plant macrofossils from the 40,000-year midden sequence. The middens represent brief, depositional episodes (mostly years to decades). Four middens represent the early to full-glacial period (40,000–18,000 cal-yr BP), eight middens are from the late-glacial/early Holocene transition (13,500–9000 cal yr BP), and 33 middens span the mid-to-late Holocene (last 7500 years). Temporal density of our Holocene middens (one every c. 210 years) is comparable with typical Holocene pollen sequences from lake sediments.

Results Early to full-glacial assemblages are characterized by low diversity and occurrence of montane conifers (*Picea pungens*, *Pseudotsuga menziesii*, *P. flexilis*, *Juniperus communis*) absent from the site today. Diversity increases in the late-glacial samples with the addition of *J. scopulorum*, *J. horizontalis*, *C. montanus*, *C. ledifolius* var. *intricatus* and mesic understory species. The coniferous trees and *J. communis* declined and *J. osteosperma* appeared during the late-glacial/Holocene transition. *Juniperus osteosperma* populations have occupied the site throughout the Holocene. *Pinus ponderosa* was established by 7500 cal-yr BP, and has occurred at least locally ever since. Montane conifers and *J. horizontalis* persisted until c. 5500 cal-yr BP. The signature events of the late Holocene were the invasions of *P. edulis* and *Ephedra viridis* and establishment of pinyon–juniper woodland in the last 800 years.

Main conclusions The Dutch John Mountain midden record adds to an emerging picture in which mid-elevation conifers (*P. flexilis*, *Pseudotsuga menziesii*, *Picea pungens*, *J. scopulorum*, *J. communis*) dominated vegetation over

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a wide area of the Colorado Plateau and adjacent Rocky Mountains. Rather than being fragmented, as often assumed in phylogeographical studies, these species had broader and more-connected distributions than they do in the region today. Paradoxically, subalpine conifers (*Picea engelmannii*, *A. lasiocarpa*) occurred at higher elevations to the south, possibly representing declining precipitation from south to north owing to southward displacement of the polar jet stream. The Dutch John Mountain record displays a series of extinction and invasion events. Most of the extinctions were local in scale; nearly all constituents of fossil midden assemblages occur within a few kilometres of Dutch John Mountain, and some occur at least locally on its slopes. The sole exception is *J. horizontalis*, which is regionally extinct. In contrast to extinctions, Holocene invasions were regional in scale; *J. osteosperma*, *P. ponderosa*, *P. edulis* and *Ephedra viridis* immigrated from glacial-age source populations far to the south.

Keywords

Extinctions, glacial, Holocene, invasions, macrofossils, phylogeography, plant distributions, pollen, woodrat middens.

INTRODUCTION

The past few decades have seen great advances in understanding of the late Quaternary biogeography of western North America. Fifty years ago, physical evidence for glacial and pluvial lake expansions, together with limited pollen evidence, were used to infer uniform lowering of vegetation zones during the last glacial period. Palaeobotanical analyses of fossil woodrat middens now indicate that this displacement was individualistic, uneven and time-transgressive (Thompson, 1988; Betancourt *et al.*, 1990). Elevational ranges of some species (especially woody species) were lowered by as much as 1000 m, while others (principally understory elements) experienced negligible change. Changes in geographical ranges were also uneven. During the last glacial period, ranges of many species (e.g. *Carnegiea gigantea*, *Larrea divaricata* var. *tridentata*, *Pinus ponderosa* var. *scopulorum*) were restricted to the extreme southern portions of their modern distributions, while the southern limits of other species extended far south of their modern boundaries (e.g. *Juniperus communis* in the northern Chihuahuan Desert and *J. scopulorum* and *J. occidentalis* in the Sonoran Desert) (see regional summaries in Betancourt *et al.*, 1990). Range expansion and contraction also occurred along longitudinal gradients [e.g. the eastward expansion of *Yucca brevifolia* during the last glacial (Van Devender, 1990b)]. Closely related species experienced role reversals between the last glacial period and the current interglacial. For example, pinyon pine species that were widespread in the glacial period became restricted in the Holocene (*P. remota*; *P. monophylla* subsp. *fallax*), while minor glacial-age species emerged as Holocene dominants (*P. edulis*, *P. monophylla* subsp. *monophylla*) (Lanner & Van Devender, 1998).

Sufficient biogeographical knowledge has now accumulated so that, given the latitude, longitude and elevation of a given site, we can often guess its glacial-age vegetation. This is

especially true for high elevations and high latitudes from pollen data (Barnosky *et al.*, 1987; Whitlock, 1993; Grimm *et al.*, 2001), and for low elevations and low latitudes based on midden data (Betancourt *et al.*, 1990). Where such predictions might fail is for low elevations at high latitudes, where there are few basins suitable for pollen studies and where, until recently, the glacial midden record remained largely unexplored. This gap overlaps with significant climatic and biogeographical boundaries in western North America, principally in the semi-arid foothills of the central Rocky Mountains (< 2200 m) between 40 and 48° N. These latitudes define a pivot point for north–south alternation of wet and dry conditions at interannual and decadal time-scales, visible in instrumental records as well as tree-ring records of precipitation spanning at least the last seven centuries (Hidalgo & Dracup, 2003). Interannual precipitation variability across western North America averages *c.* 10% of the mean, and is mostly determined by precipitation variations between 40 and 45° N (Dettinger *et al.*, 1998). Precipitation variability in this region is often asynchronous between low and high elevations, with low elevations responding to Pacific variability (El Niño–Southern Oscillation and Pacific Decadal Oscillation) more like the south-western USA, and higher elevations more like the Pacific Northwest (Hidalgo & Dracup, 2003; Gray *et al.*, 2004a). These contrasts in precipitation variability may decouple cross-regional plant population dynamics at all time-scales, and may explain abrupt ecotones evident across altitudinal and latitudinal gradients. It is not surprising therefore that many plant species (e.g. *P. ponderosa* var. *scopulorum*, *P. edulis*, *P. contorta*, *Abies concolor*, *J. osteosperma*, *J. horizontalis*, *Ephedra viridis*, *C. ledifolius* var. *ledifolius*, *C. ledifolius* var. *intricatus*) reach their regional limits in the region.

As part of an ongoing, systematic effort to extend midden coverage into this important climatic and biogeographical transition (e.g. Lyford *et al.*, 2002, 2003; Jackson *et al.*, 2002),

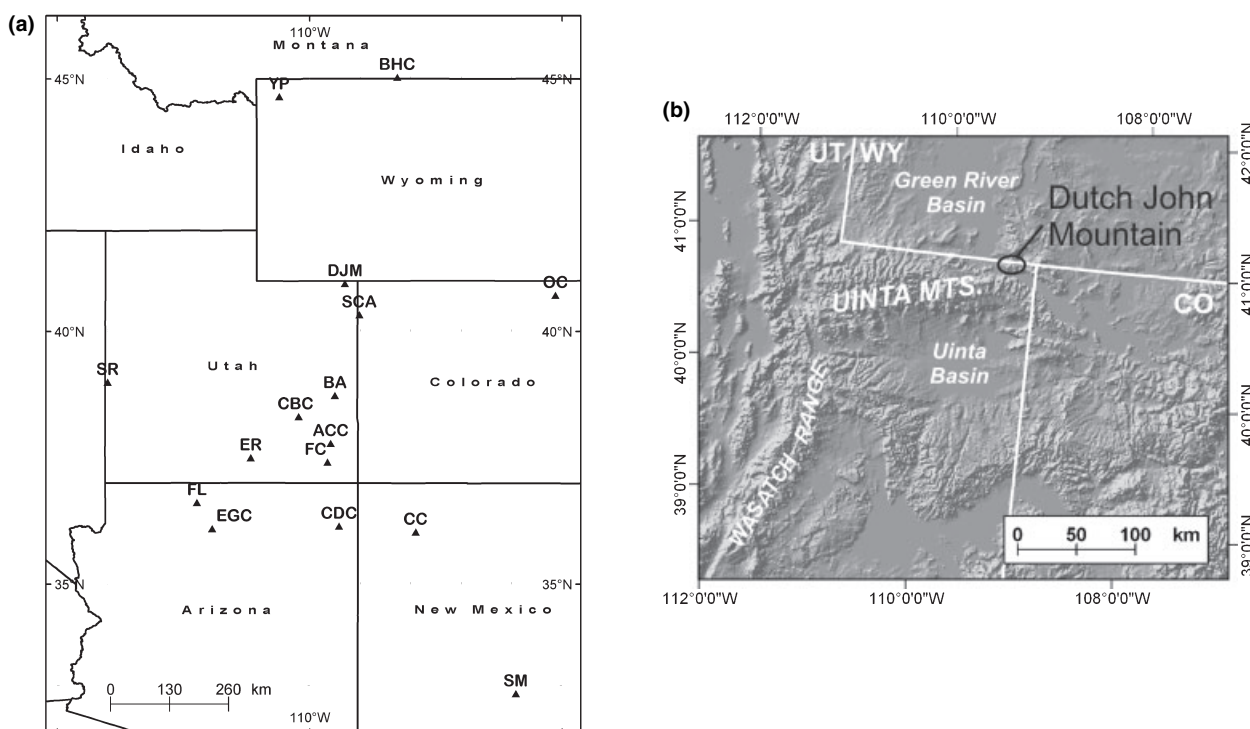


Figure 1 (a) Interior western United States, showing locations of palaeoecological study sites mentioned in text. DJM, Dutch John Mountain. Other sites, from north to south, are: BHC, Bighorn Canyon; YP, Yellowstone Plateau; OC, Owl Canyon; SCA, Sand Canyon Alcove; SR, Snake Range; BA, Bison Alcove; CBC, Cowboy Cave; ACC, Allen Canyon Cave; ER, Escalante River region; FC, Fishmouth Cave; FL, Fracas Lake; EGC, Eastern Grand Canyon; CDC, Canyon de Chelly; CC, Chaco Canyon; SM, Sacramento Mountains. Harmony Flat Shelter, Cottonwood Cave and Falling Arch (not shown) are all in the vicinity of Fishmouth Cave (FC). Long Canyon Cave and Bechan Cave (not shown) are in the vicinity of the ER. (b) West-central Rocky Mountain region, showing location of Dutch John Mountain site in relation to important physiographical features.

we developed a record from Dutch John Mountain on the north-eastern flanks of the Uinta Mountains along the Utah/Wyoming border (Fig. 1). The 46-midden series spans the past 40,000 years and has unusually high temporal density of samples for most of the Holocene and much of the late-glacial period. Several dominant trees meet their geographical limits in the immediate area. The northernmost populations of pinyon pine (*P. edulis*) are a few kilometres north of Dutch John Mountain, although a small, isolated population of *P. edulis/P. monophylla* hybrids has been documented from the Crawford Mountains 100 km NW (Lanner & Hutchison, 1972). The northernmost pinyon-dominated woodland occurs on the Dutch John escarpment, and the northernmost populations of ponderosa pine (*P. ponderosa* var. *scopulorum*) in the Colorado/Green River drainage also occur on Dutch John Mountain. Our midden records provide information on the Holocene migration history of these and other species, and show how woodland vegetation at the site has developed during the past 9500 years in response to environmental changes and natural invasions. The pre-Holocene middens also provide direct evidence of the Wisconsinan and late-glacial biogeography of the central Rocky Mountain region, which is very poorly known, and indicate the timing of climatic changes and local extinctions of montane tree species at the site.

STUDY SITE

Geology and physiography

The study area is on the north-eastern slope of the Uinta Mountains, which are bounded by the Green River Basin to the north and the Uinta Basin to the south (Fig. 1). The Uintas are unusual in western North America in that the primary axis of the range trends east/west, rather than north/south. They reach their highest elevations (to 4126 m) in the western half of the range, which was extensively glaciated (Stokes, 1986). The unglaciated eastern Uinta Mountains are lower (< 3000 m), with rounded crests and extensive plateau-like surfaces (Hansen, 1986).

Dutch John Mountain (Fig. 2) is a prominent escarpment of Navajo Sandstone, an aeolian sandstone of Triassic/Jurassic age (Hansen, 1965). The ridge is part of a nearly continuous line of south-facing cliffs running along an east/west axis for a length of 32 km. The Navajo Sandstone is nearly vertically oriented at Dutch John Mountain, forming cliffs 30–100 m high along the south face (Fig. 3). South of Dutch John Mountain, the landscape consists of highly dissected Uinta Mountain Group sandstones and quartzites, sloping gently southward 3–4 km to the rim of Red Canyon (1890 m) of

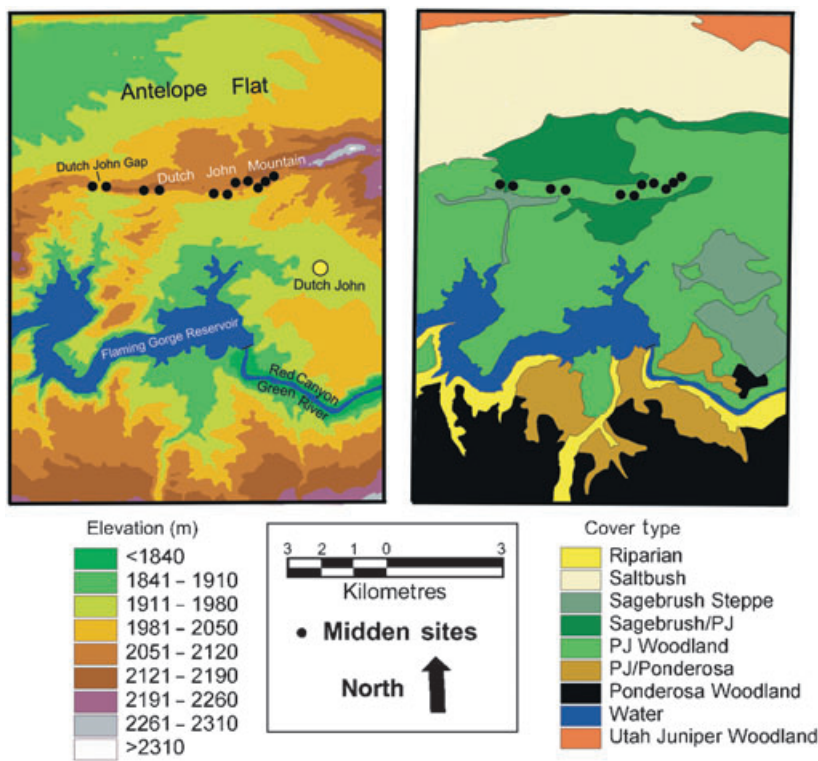


Figure 2 (a) Elevation map of the Dutch John 7.5' USGS topographic Quadrangle. (b) Vegetation map of Dutch John 7.5' USGS topographic Quadrangle, adapted from the Ecological Units Inventory of the Ashley National Forest, with modifications based on personal observations by S.T. Jackson and S.T. Gray. The abbreviation PJ refers to pinyon/juniper (*Pinus edulis*/*Juniperus osteosperma*) woodlands. Black dots denote individual woodrat-midden localities.

the Green River (river elevation 1710 m), which is partly inundated by Flaming Gorge Reservoir (mean pool elevation 1842 m) (Fig. 2a). These gentler slopes comprise the Dutch John Bench, which is locally capped by Miocene sandstones and tuffs (Hansen, 1986). The Antelope Flat area north of the mountain is a gently sloping landscape of Cretaceous shales and Quaternary valley fill, alluvium and aeolian sands (Hansen, 1965). The sole break in the cliff face of Dutch John Mountain is at Dutch John Gap (Fig. 2a), a cut c. 50 m wide with a base elevation of 1980 m.

Climate

Mean July temperatures at Flaming Gorge Dam (1845 m elevation), 4 km south of Dutch John Mountain, are 29.7 °C (Fig. 4) (1957–2000; <http://www.wrcc.dri.edu>). July temperatures only occasionally exceed 35 °C. Mean January temperatures are –5.5 °C, with occasional low extremes of –25 °C. Daytime temperatures in January frequently exceed 2 °C. The meteorological station at Flaming Gorge Dam receives on average 32 cm of precipitation per year (range 17.6–45.1, SD 6.5) from frontal systems, lows aloft and



Figure 3 Photograph of the south slope of Dutch John Mountain, c. 300 m east of Dutch John Gap (S.T. Jackson, August 2000). Slopes are vegetated by pinyon/juniper woodlands. Middens were collected from caves and crevices along the cliff faces and adjacent draws and ravines.

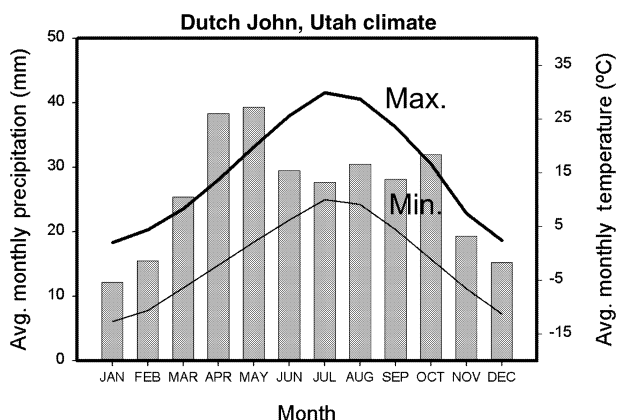


Figure 4 Seasonal pattern of monthly precipitation, mean minimum temperature, and mean maximum temperature at Flaming Gorge Dam, Utah, 40°56' N, 109°25' W, 1845 m elevation), 4 km south of our study site. Period of record shown is 1957–2003 (<http://www.wrcc.dri.edu/>).

thunderstorms. Frontal storms in winter (December–February) account for < 14% of total annual precipitation at Flaming Gorge Dam (Fig. 4). Precipitation is reduced from descent and weakening of fronts as they pass from the Wasatch and Uinta Mountains eastward into the Uinta Basin and to Dutch John Mountain. When they enter from the south-west, frontal storms occasionally can yield more than 25 cm of annual snowfall on basin floors, with higher amounts on the Uinta flanks.

Peak precipitation in the Dutch John area occurs in late spring (April–June), similar to the central Rockies and western Great Plains, but contrasting with the arid foresummer typical of regions to the south. Lows aloft are a key source of sometimes heavy and/or widespread precipitation in the spring (April–June) and fall (September–October), and occur more commonly during El Niño episodes. In June–September, thunderstorms deliver significant but heterogeneously distributed precipitation in the Dutch John area, which is at the northern end of the south-west monsoon (Mock, 1996; Adams & Comrie, 1997; Higgins *et al.*, 1998). Substantial spring/summer droughts have occurred in the past century, and the region has experienced severe drought conditions since 1999. Nevertheless, tree-ring records from the region show that the entire twentieth century, and the period 1965–98 in particular, was very wet compared with the previous seven centuries (Gray *et al.*, 2004b).

The study area is located within the north–south boundary region of the bipolar response to ENSO during the cold season (Dettinger *et al.*, 1998; Hidalgo & Dracup, 2003). Within this boundary region, the correlation between ENSO indicators and cold season precipitation shifted around 1932/33 from negative (i.e. dry during El Niño events, like the Pacific Northwest) to positive (i.e. wet during El Niño events, like the Southwest). It is unclear how millennial-scale variability would have affected inter-

decadal variability and the bipolar response to ENSO and Pacific climate. The entire boundary region might have shifted north or south at various times in the Holocene, alternatively synchronizing climate variability at Dutch John Mountain with the Pacific Northwest and the south-western USA.

Flora and vegetation

The Uinta Range and adjacent foothills span a broad vegetational gradient, with upper slopes and summits vegetated by alpine tundra (> 3350 m) through subalpine *Picea engelmannii*/*A. lasiocarpa* forest (3200–3500 m) and montane *P. contorta* forest (2400–3200 m) (Svilha, 1932; Graham, 1937; Knight, 1994). The southern and eastern flanks of the Uintas, which have relatively high summer precipitation, have extensive *P. ponderosa* forests (1900–2500 m) and pinyon–juniper woodlands (*P. edulis*, *J. osteosperma*) (1675–2200 m) grading downward into sagebrush steppe and desert shrubland (Graham, 1937; Hansen, 1965). *Pinus ponderosa* forests, pinyon–juniper woodlands, and *J. osteosperma* woodlands also occur on the north slope of the range, south and west of the study site. Further west, *P. contorta* forests grade downslope into mixed forests dominated by *Pseudotsuga menziesii* and *Populus tremuloides*, which in turn give way to sagebrush steppe and desert shrubland below 2000 m.

Vegetation of the Dutch John Mountain region consists of a mosaic of sagebrush steppe, desert shrubland, pinyon–juniper woodland and ponderosa pine forest (Fig. 2b). The south-facing slope of Dutch John Mountain is vegetated by moderately dense (15–30% crown cover) pinyon/juniper woodlands dominated by *P. edulis* (40–95% of total woody-plant crown coverage) (Figs 2b & 3). *Juniperus osteosperma* and *C. ledifolius* var. *intricatus* occur as subdominants (up to 30% crown coverage). Other woody plants include *C. ledifolius* var. *ledifolius*, *C. montanus*, *Ephedra viridis*, *Philadelphus microphyllus*, *Chrysothamnus nauseosus*, *Purshia tridentata* and *Leptodactylon pungens*, which all occur as scattered low shrubs. Scattered individuals of *P. ponderosa* grow near the eastern part of the ridge, and on gentle slopes south of the escarpment. Individuals of *J. scopulorum* and *Acer glabrum* occur locally on deeply shaded sites between boulders and in ravines, and we observed one *Pseudotsuga menziesii* tree growing in a sheltered ravine. Much of the woodland on the south-facing slope is old-growth; live pinyons 500–750 years old have been documented over much of Dutch John Mountain, particularly on the east side (Gray, 2003). Extensive areas of pinyon–juniper and ponderosa pine woodlands on and around Dutch John Mountain were destroyed by the human-caused Mustang Fire in early July 2002. The fire extended over the eastern third of the south slope of Dutch John Mountain, destroying the oldest pinyon–juniper stands, and burned extensively in woodlands to the south and east of the ridge. This is probably the first stand-replacing fire that has burned at this site in the past several centuries.

Graminoids and forbs are sparse in the woodlands. *Carex rossii*, *Stipa hymenoides*, *Bromus tectorum*, and *Opuntia polyacantha* are widespread; *Poa secunda*, *P. fendleriana*, *Elymus spicatus*, *Galium multiflorum*, *Streptanthus cordatus*, *Trifolium andinum*, *Descurainia pinnata*, and *Eriogonum ovalifolium* occur infrequently. *Artemisia tridentata* ssp. *wyomingensis* dominates locally on deep-soiled flats below the escarpment.

Pinyon–juniper woodlands occur on the gentle slopes of the north side of Dutch John Mountain, and are invading adjacent sagebrush steppe at the base of the slope. Scattered individuals of *Pseudotsuga menziesii* occur on the north-facing backslope near the crest. Vegetation of Antelope Flat, a low-lying area immediately north of Dutch John Mountain, consists of sparse pinyon–juniper woodland on sandstone escarpments, sagebrush steppe (dominated by *Artemisia tridentata* var. *wyomingensis*) on low-salinity soils, and desert shrubland (dominated by *Atriplex gardnerii*) on saline soils (Fig. 2b). *Sarcobatus vermiculatus* occurs locally in poorly drained saline flats.

Pinyon–juniper woodlands, occasionally intermixed with *P. ponderosa*, extend south of Dutch John Mountain to the bottom of Red Canyon along the Green River (1710 m) (Fig. 2b). Slopes of the south face of Red Canyon are occupied by *P. ponderosa* and pinyon–juniper woodland, with *Pseudotsuga menziesii*, *P. flexilis* and *J. scopulorum* occurring locally on mesic sites (steep shaded slopes, drainages, riparian zones) (Fig. 2b). *Picea pungens* probably grew as a riparian tree along the Green River prior to flooding of Flaming Gorge Reservoir (Hansen, 1965; Sherel Goodrich, Ashley National Forest, pers. comm.). North-facing slopes above the canyon are vegetated by woodlands of *P. ponderosa*/pinyon–juniper, grading into open *P. ponderosa* forests above 2010–2075 m.

METHODS

We collected 60 woodrat middens from a 4500-m length of the south slope of Dutch John Mountain (Figs 2 & 3), an area bounded by 40°57'14" N, 40°57'21" N, 109°24'30" W and 109°28'20" W. Middens were collected from bedrock overhangs, crevices, and shallow caves in Navajo Sandstone, with clusters of 5–10 middens coming from three of the caves. All the middens came from the south-facing slope, except for a few middens from the east- (nos. 607–611 and 617–619) and west-facing slopes (nos. 613–616) of Dutch John Gap (Fig. 2). Elevations ranged from 2013 to 2075 m. Vegetation surrounding all of the midden sites consisted of *P. edulis*/*J. osteosperma* woodlands. Scattered individuals of *P. ponderosa* grow within 100 m of a few of the midden sites on the eastern end of the study area.

Middens were collected, cleaned and prepared for macrofossil analysis according to methods described in Spaulding *et al.* (1990) and Lyford *et al.* (2002). Identifications were based on comparison with herbarium-documented reference specimens at the University of Wyoming Quaternary Plant Ecology Laboratory and the University of Arizona's Desert Laboratory. Each plant taxon in each midden was assigned a

relative abundance value (1, single occurrence; 5, dominant) (Spaulding *et al.*, 1990).

We analysed 26 of the middens for pollen. Pollen samples, each consisting of a 10–20 cm³ block from the interior of the midden, were soaked in water until completely dispersed, and then sieved (180 *µm* mesh) to remove coarse particles. The remaining liquid was stirred thoroughly. Thirty seconds after stirring had ceased, we sampled the entire vertical profile of the liquid using a 100-mL pipette. This sample was centrifuged, and then processed for pollen extraction using standard procedures for organic- and mineral-rich sediments (Jackson, 1999). Each pollen sample was counted beyond a sum of 300 terrestrial pollen grains. Pollen percentages were calculated based on a sum of terrestrial pollen types (including all tree, shrub, herb and graminoid morphotypes). Subgeneric differentiation of *Pinus* pollen grains was based on morphological criteria of Hansen & Cushing (1973).

A total of 48 middens were selected for radiocarbon dating, based on midden integrity and composition. We obtained conventional ¹⁴C dates on samples of *Neotoma* faecal pellets (c. 3–10 g) from 30 middens, accelerator mass spectrometry (AMS) ¹⁴C dates on *Neotoma* faecal pellets from 9 middens, and AMS dates on *J. osteosperma* or *P. edulis* foliage from 10 middens (Table 1). AMS-dating provides precise dates from small amounts of organic material, and hence yielded direct age-estimates for macrofossils from the middens, which helped pinpoint first occurrences of *J. osteosperma* and *P. edulis*. Although in previous studies (Betancourt *et al.*, 2001; Jackson *et al.*, 2002; Lyford *et al.*, 2002) we have used AMS dating to address potential problems of midden contamination or temporal-mixing, we did this for only one midden (no. 559) in the current study. All other middens lacked indications of contamination or mixing.

AMS targets were prepared at the Desert Laboratory in Tucson, where samples were pretreated to remove carbonates and acid- and base-soluble organic matter. Samples were then combusted to CO₂ on a vacuum line, converted to graphite, and pressed into targets. AMS targets were measured for ¹⁴C activity at the University of Arizona-NSF Accelerator Facility.

Radiocarbon ages for all samples dating < 20,000 ¹⁴C yr BP were converted to calendar-year ages using the Intcal 98 calibration curve, based on Method A (ranges with intercepts) from CALIB 4.3 (Stuiver & Reimer, 1993). Calendar-year age estimation for samples dating ≥ 20,000 ¹⁴C yr BP is less certain; calibration models are still being improved and refined as new data sets become available (Jöris & Weninger, 1998; Kitagawa & van der Plicht, 1998), and hence precise calendar-year age-estimates are subject to some change. We used the CalPal program (<http://www.calpal.de>) for calendric age-conversion of our three samples predating 20,000 ¹⁴C yr BP. All ages discussed in this paper are calendar-year ages (years before present, 0 = 1950 AD) unless otherwise indicated. In two cases, midden samples from the same locality that were judged in the field to represent discrete units yielded similar radiocarbon dates (not significantly different at *P* < 0.5 using the *F*-test of

Table 1 Radiocarbon ages of middens analysed from Dutch John Mountain

Midden no.	Laboratory no.	Age (^{14}C yr BP)	Age (cal-yr BP)*	Material dated
617	AA36764	375 ± 40	465 (310–510)	<i>Pinus edulis</i> needles
562	GX26341	410 ± 50	500 (315–530)	<i>Neotoma</i> faecal pellets
559	GX26339	460 ± 50	510 (340–550)	<i>Neotoma</i> faecal pellets
559	AA36759	570 ± 40	615 (515–650)	<i>Pinus edulis</i> needles
616	AA36767	620 ± 40	595 (540–660)	<i>Pinus edulis</i> needles
613B	GX26241	880 ± 130	775 (560–1055)	<i>Neotoma</i> faecal pellets
613B	GX26273	1080 ± 70	970 (800–1170)	<i>Neotoma</i> faecal pellets
202B	AA33675	1070 ± 55	965 (805–1165)	<i>Juniperus osteosperma</i> foliage
621	GX26245	1380 ± 90	1290 (1090–1475)	<i>Neotoma</i> faecal pellets
323	AA33388	1495 ± 35	1370 (1305–1510)	<i>Juniperus osteosperma</i> foliage
569	GX26342	1630 ± 70	1530 (1350–1705)	<i>Neotoma</i> faecal pellets
620	GX26244	1740 ± 90	1660 (1415–1870)	<i>Neotoma</i> faecal pellets
327	AA33390	1985 ± 50	1905 (1825–2040)	<i>Juniperus osteosperma</i> foliage
622	GX26274	1990 ± 70	1940 (1815–2120)	<i>Neotoma</i> faecal pellets
614	GX26346	2170 ± 70	2150 (1950–2345)	<i>Neotoma</i> faecal pellets
303	AA33384	2255 ± 50	2315 (2125–2350)	<i>Juniperus osteosperma</i> foliage
570	GX26343	2610 ± 50	2750 (2545–2780)	<i>Neotoma</i> faecal pellets
561	GX26340	2630 ± 60	2750 (2550–2850)	<i>Neotoma</i> faecal pellets
558B	AA36762	2760 ± 45	2850 (2765–2950)	<i>Neotoma</i> faecal pellets
555B	GX26239	2900 ± 130	3055 (2755–3380)	<i>Neotoma</i> faecal pellets
321A	AA33387	2945 ± 70	3130 (2875–3340)	<i>Juniperus osteosperma</i> foliage
556A	GX26338	3420 ± 80	3660 (3470–3870)	<i>Neotoma</i> faecal pellets
556B	GX26265	3770 ± 70	4110 (3925–4410)	<i>Neotoma</i> faecal pellets
618B	GX26243	4000 ± 170	4490 (3935–4870)	<i>Neotoma</i> faecal pellets
619	GX26348	4100 ± 60	4570 (4420–4830)	<i>Neotoma</i> faecal pellets
615	GX26347	4210 ± 50	4825 (4555–4855)	<i>Neotoma</i> faecal pellets
574	AA36770	4635 ± 55	5420 (5085–5575)	<i>Neotoma</i> faecal pellets
326	AA33383	4650 ± 85	5415 (5050–5590)	<i>Juniperus osteosperma</i> foliage
573	AA36765	4805 ± 50	5495 (5330–5635)	<i>Neotoma</i> faecal pellets
572A	AA36763	5015 ± 65	5740 (5605–5915)	<i>Juniperus osteosperma</i> foliage
608	AA36761	5140 ± 100	5910 (5655–6170)	<i>Neotoma</i> faecal pellets
560	AA36760	5595 ± 75	6365 (6210–6530)	<i>Neotoma</i> faecal pellets
610	AA36769	5635 ± 55	6410 (6300–6530)	<i>Neotoma</i> faecal pellets
611	GX26272	5850 ± 100	6710 (6410–6890)	<i>Neotoma</i> faecal pellets
618A	GX26242	6290 ± 140	7245 (6800–7460)	<i>Neotoma</i> faecal pellets
328	AA33391	8455 ± 75	9485 (9480–9550)	<i>Juniperus osteosperma</i> foliage
607B	GX26345	9100 ± 70	10,235 (10,160–10,470)	<i>Neotoma</i> faecal pellets
607A2	GX26270	9390 ± 110	10,615 (10,245–11,090)	<i>Neotoma</i> faecal pellets
607A1	GX26240	9530 ± 280	10,980 (10,180–11,685)	<i>Neotoma</i> faecal pellets
325B	GX25590	9640 ± 140	11,110 (10,560–11,260)	<i>Neotoma</i> faecal pellets
571	GX26344	10180 ± 140	11,815 (11,235–12,725)	<i>Neotoma</i> faecal pellets
607C	GX26271	10,190 ± 110	11,810 (11,265–12,585)	<i>Neotoma</i> faecal pellets
572D	GX26268	10570 ± 120	12,740 (11,965–12,950)	<i>Neotoma</i> faecal pellets
572B	GX26267	10590 ± 110	12,735 (12,105–12,955)	<i>Neotoma</i> faecal pellets
322	GX25593	11,150 ± 300	13,145 (12,430–13,820)	<i>Neotoma</i> faecal pellets
325C	GX25783	15,730 ± 320	18,780 (17,880–19,745)	<i>Neotoma</i> faecal pellets
609A	AA36768	23,130 ± 190	26,858 (26,592–27,124)	<i>Neotoma</i> faecal pellets
325A	GX25782	26,360 ± 620	29,851 (29,409–30,293)	<i>Neotoma</i> faecal pellets
609B	AA36766	35,170 ± 710	39,971 (39,163–40,778)	<i>Neotoma</i> faecal pellets

*Age estimates include the median intercept and (in parentheses) minimum and maximum ages based on 2 standard deviations from minimum and maximum intercepts.

Long & Rippeteau, 1974). In these cases (607A1 and 607A2; 572B and 572D), we concluded that the samples represented the same midden unit and pooled the pollen and macrofossil

data. We averaged the radiocarbon age estimates (Long & Rippeteau, 1974) for these pairs of samples (Table 1) before converting to calendar-year ages.

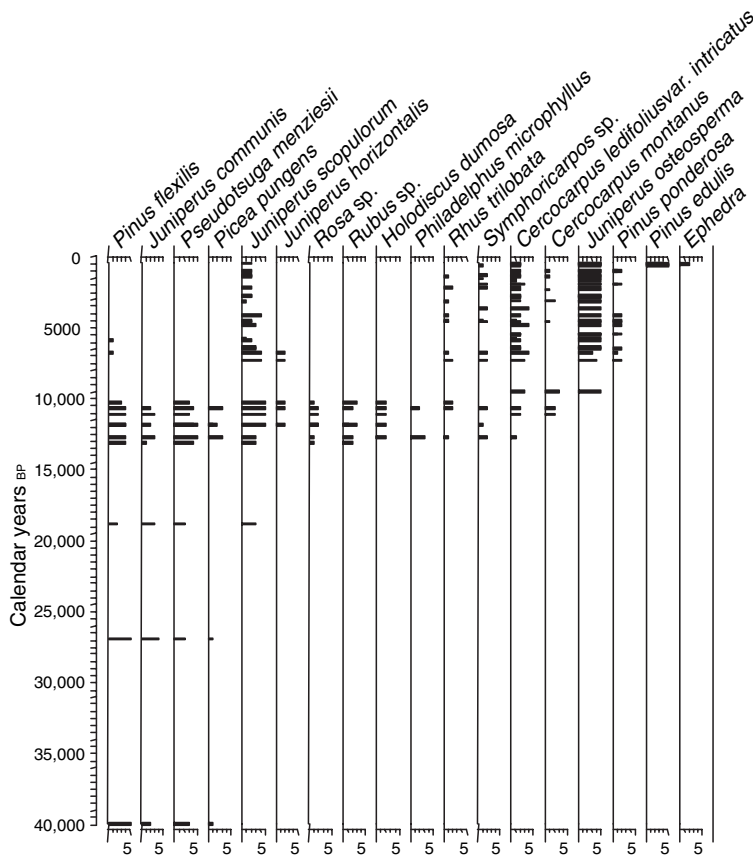


Figure 5 Relative abundances (1–5) of plant macrofossils of conifers and tall shrubs from fossil woodrat middens at Dutch John Mountain.

RESULTS

Radiocarbon dating

The 45 dated middens fell into three general time-clusters (Table 1): Wisconsinan (40,000–18,500 yr BP; 4 middens), late-glacial/Holocene transition (13,500–9000 yr BP; 8 middens), and mid-late Holocene (< 7500 yr BP; 33 middens). The four Wisconsinan middens are widely spaced in time, spanning more than 20,000 years. The late-glacial middens, separated from the Wisconsinan middens by 5600 years, are more tightly spaced, with no more than 930 years separating any two middens. A 2200-year gap separates the late-glacial group from the Holocene group, which has very high temporal density (33 samples spanning 7250 years; no gaps > 590 years; median gap between adjacent samples is 164 years). Temporal density of our Holocene samples (averaging one sample per 213 years) is comparable with typical Holocene pollen sequences from lake sediments (Webb, 1993).

Late Wisconsinan (40,000–18,500 yr BP): montane conifer woodlands

The four Wisconsinan middens were characterized by low species diversity and by dominance of woody conifers that grow in the region today at substantially higher elevations

(*P. flexilis*, *Pseudotsuga menziesii*, *Picea pungens*, *J. communis*) (Figs 5 & 6). The youngest midden (18,780 yr BP) also had macrofossils of *J. scopulorum*, which is restricted to mesic sites (ravines, draws, seepages) across the region (from Red Canyon at 1710 m to lower slopes of the Uintas at 2500 m). Macrofossils of conifers and most shrubs were completely absent in one midden, 325A (30,040 yr BP), and sparsely represented in another, 325C (18,780 yr BP) (Fig. 5). These middens were both from a small cave on a south-facing cliff on the east end of Dutch John Mountain. Woodrats generally collect material from coniferous trees and shrubs when they are nearby (Lyford *et al.*, 2004), so sparseness or absence of macrofossils from these middens indicates absence from the surrounding landscape. Pollen assemblages from 325A and 325C, however, are dominated by Cupressaceae and *Pinus* (mainly *P. flexilis*; pollen of *Pinus* subgenus *Pinus*, which includes *P. contorta* and *P. ponderosa*, is rare) (Fig. 7) suggesting abundant woody vegetation nearby, perhaps on mesic microhabitats on the slopes of Dutch John Mountain. Other important elements include *Artemisia*, Chenopodiaceae and other non-woody pollen types, which probably derive from both plants on the nearby slopes and from steppe or scrubland in surrounding lowlands (Tables 3 and 4).

The other two middens, 609B (39,820 yr BP) and 609A (26,310 yr BP), were from a cave on an east-facing cliff in

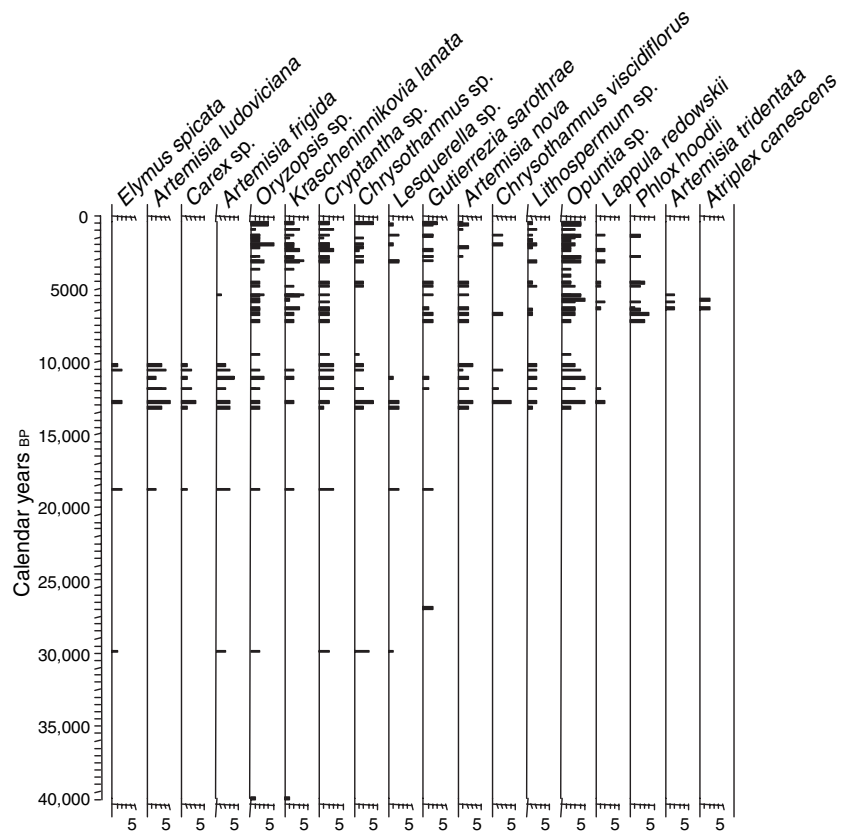


Figure 6 Relative abundances (1–5) of plant macrofossils of low shrubs, herbs, graminoids and cacti from fossil woodrat middens at Dutch John Mountain.

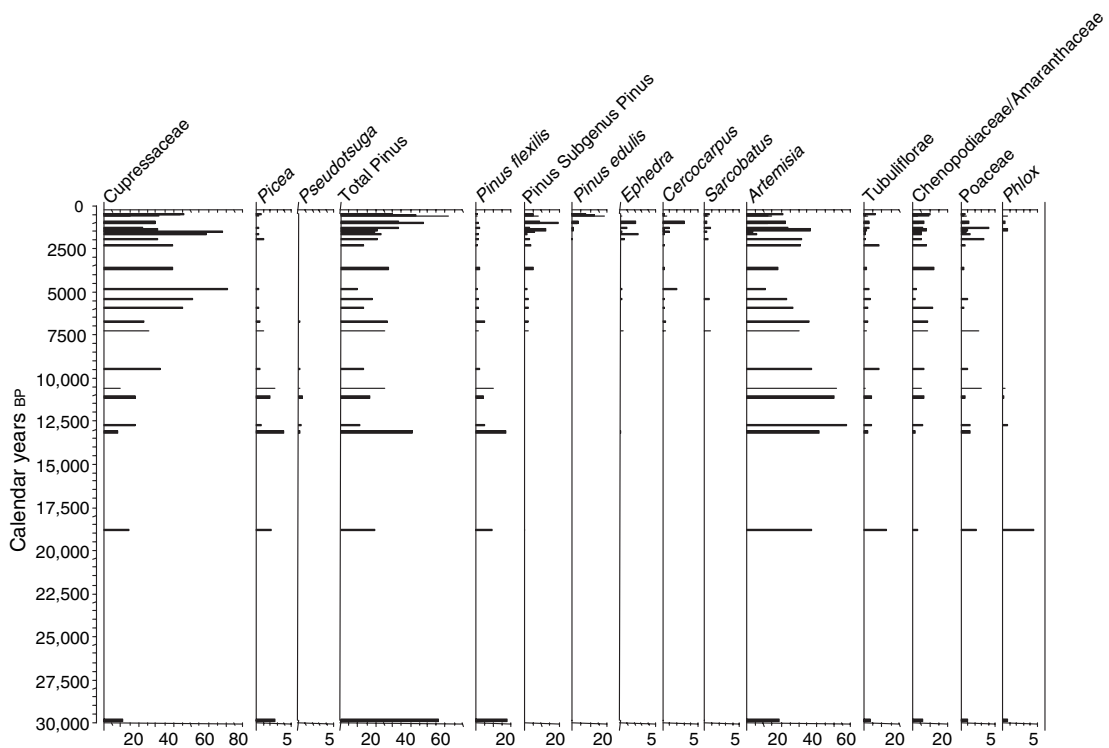


Figure 7 Percentages of major pollen types from woodrat middens at Dutch John Mountain. Note expanded scale for uncommon types (*Picea*, *Pseudotsuga*, *Ephedra*, *Cercocarpus*, *Sarcobatus*, *Poaceae*, *Phlox*).

Dutch John Gap. Unfortunately pollen samples were not obtained from these middens, but they did have abundant conifer macrofossils (Fig. 5). Variation in conifer macrofossil abundance in the Wisconsinan middens may represent centennial to millennial scale climatic variations during this period (e.g. Benson, 2004) or effective-moisture differences between sites.

Late-glacial/early Holocene (13,500–9500 yr BP): mesic montane conifers and transition to Holocene juniper woodlands

Plant macrofossil assemblages from the late-glacial period are generally more diverse than the Wisconsinan assemblages (Figs 5 & 6). *Pinus flexilis*, *Pseudotsuga menziesii*, and *J. communis* remain abundant until c. 10,500 yr BP, and *J. scopulorum* occurs in all middens except the youngest (9490 yr BP) (Fig. 5). *Picea pungens* is present between 12,740 and 10,600 yr BP, and *J. horizontalis* occurs from 11,815 to 10,235 yr BP (Fig. 5). All of these montane/boreal conifers are absent from the youngest midden (9490 yr BP), although they occur in some early Holocene middens. *Pseudotsuga*, *P. flexilis*, *J. communis*, and *J. scopulorum* are well-represented in midden 325B (11,110 yr BP), which is from the same site as the two Wisconsinan middens where conifers are poorly represented (Fig. 5). This, together with the consistent occurrence of *Rosa*, *Rubus*, *Holodiscus*, *Philadelphus*, *Artemisia ludoviciana*, *Artemisia frigida* and *Carex* (Figs 5 & 6), indicates that late-glacial conditions were wetter than during the Wisconsinan. Pollen assemblages, dominated by *Pinus* (mainly *P. flexilis*), Cupressaceae, *Artemisia* and Chenopodiaceae/Amaranthaceae (Fig. 7), suggest conifer-dominated woodlands with extensive open areas (*Artemisia*, Chenopodiaceae). Macrofossils indicate that *Artemisia*, grasses and forbs occurred locally, but much of the pollen from non-woody plants may also have derived from Antelope Flats and similar areas with fine-textured soils.

Vegetation on Dutch John Mountain underwent a transition from late-glacial montane conifers (*Pseudotsuga menziesii*, *P. flexilis*, *Picea pungens*, *J. scopulorum*) to Holocene juniper woodlands (*J. osteosperma* with *J. scopulorum* and *Cercocarpus* spp.) between 10,500 and 7500 yr BP (Figs 5 & 6). Unfortunately, temporal density is particularly sparse during this critical interval. Increasingly warm and/or dry conditions by 11,100 yr BP are implied by the appearance of *C. ledifolius* var. *intricatus* and *C. montanus* (Fig. 5); both grow on the south slope of Dutch John Mountain today. The montane conifers persisted locally until at least 10,610 yr BP, but *Picea pungens* disappeared by 10,235 yr BP (Fig. 5). *Pseudotsuga* macrofossils occur in small numbers in a few mid-Holocene middens, probably representing persistence of isolated individuals or populations on mesic microsites.

Continued decrease in effective moisture and increase in temperature are implied by the appearance of *J. osteosperma* in a midden dated 9490 yr BP. That midden has no other coniferous species represented, although both *C. ledifolius* var. *intricatus* and *C. montanus* occur (Fig. 5). The low woody-plant diversity and the absence of *J. scopulorum* may represent

unusually dry conditions at this time. Sharpe (1991, 2002) observed a similar transition towards drier conditions in a three-midden series at Sand Canyon Alcove in NW Colorado, where a diverse late-glacial assemblage (11,230 yr BP) of montane conifers was joined by *J. osteosperma* 10,215 yr BP. Only *J. osteosperma*, *J. scopulorum* and *P. flexilis* remained by 9490 yr BP (Sharpe, 2002).

Mid-late Holocene (7500 yr BP to present): static juniper woodlands and late Holocene pinyon invasion

All of the Holocene midden assemblages are dominated by *J. osteosperma*, and most have *C. ledifolius* var. *intricatus* as a subdominant (Fig. 5). *Juniperus scopulorum* also occurs in slightly more than half of the Holocene middens. It is more consistently represented, and in greater abundance, in mid-Holocene middens (7500–5500 yr BP) (Fig. 5). Macrofossils of *Pseudotsuga menziesii*, *P. flexilis* and *J. horizontalis* also occur in the two oldest middens (7250 and 6710 yr BP) in the mid/late Holocene series. *Pinus ponderosa* occurs sporadically in the entire mid/late Holocene series, including the oldest midden (7250 yr BP), and occurs most consistently before 4000 yr BP (Fig. 5). Presence/absence of *J. scopulorum* and *P. ponderosa* in the series may be related to differences among middens in local environment (aspect, proximity to draws, etc.). However, their higher abundance and more consistent occurrence before 4000 yr BP (Fig. 5) suggest that conditions may have been moister than today. Many of the species consistently represented in late-glacial assemblages, including shrubs (*J. communis*, *Rosa*, *Rubus*, *Holodiscus*, *Philadelphus*, *Artemisia ludoviciana*) and graminoids (*Elymus spicatus*, *Carex*), are absent from all Holocene middens (Figs 5 & 6). However, other shrubs (*Rhus*, *Symphoricarpos*, *Cercocarpus* spp., *Artemisia nova* and other Asteraceae), herbs (*Krascheninnikovia*, *Cryptantha*, *Lithospermum*, *Lappula*), graminoids (*Oryzopsis*), and succulents (*Opuntia*) occur in the late-glacial and Holocene (Figs 5 & 6). The only new species appearing in the mid-Holocene are *P. ponderosa*, *Phlox hoodii*, *Artemisia tridentata* and *Atriplex canescens* (Fig. 6). The latter two disappear from the midden record after 6000 yr BP, although they occur near Dutch John Mountain today.

Holocene pollen assemblages are dominated by Cupressaceae, *Pinus*, *Artemisia* and Chenopodiaceae (Fig. 6). Pollen of *Pinus* subgenus *Pinus* is abundant in most middens, probably representing *P. ponderosa* populations on the north-facing slopes above Red Canyon (Fig. 2b) as well as scattered individuals on and near Dutch John Mountain. *Pinus flexilis*-type pollen occurs in trace amounts (< 5% in all but one sample), primarily in middens predating 3500 yr BP (Fig. 7).

Pinus edulis macrofossils are absent from all Dutch John middens predating 775 yr BP, but occur in all middens younger than 615 yr BP (Fig. 5). This pattern is supported by the pollen data, which show near-absence of *P. edulis*-type pollen in all middens 1300 yr BP and older, first occurrence at low percentages 970 yr BP, and relatively high percentages (5–15%) in middens ≤ 615 yr BP (Fig. 7). *Ephedra* macrofossils are absent

from middens older than 500 yr BP (Fig. 5), and *Ephedra* pollen occurs in trace amounts until 2000 yr BP, when it increases (Fig. 7). Macrofossils of both *P. edulis* and *Ephedra* are consistently represented in middens when populations are nearby; the probability of occurrence in a midden given occurrence of individuals within 50 m is 70–80% for both species (Lyford *et al.*, 2004). In view of the temporal density of Holocene middens from the study area, and the corroboration from pollen evidence, we conclude that both *P. edulis* and *Ephedra viridis* are recent immigrants to Dutch John Mountain.

Pinus edulis is sparse north of Dutch John Mountain; a few scattered individuals occur in juniper woodlands north of Antelope Flat (Fig. 2) and are completely absent 10 km north. Our study area has the northernmost woodland dominated by *P. edulis*. The nearest populations south of Red Canyon are 40 km south, near Vernal, Utah. Our midden data provide strong evidence for recent invasion of the study area by *P. edulis*, commencing no more than 1000 yr BP (Figs 5 & 7). *Pinus edulis* currently spans a broad elevational gradient in the study area, from 1710 m at the bottom of Red Canyon to 2200 m at the summit of Dutch John Mountain. Although our midden samples cover only the uppermost portion of this elevational range (2013–2075 m), our pollen data indicate that the entire Dutch John/Red Canyon area was invaded by *P. edulis* in the late Holocene. *Pinus* pollen is well-dispersed and abundantly produced (Jackson & Lyford, 1999), and the absence of *P. edulis* pollen from middens predating 1000 yr BP (Fig. 7) provides strong evidence that populations did not occur anywhere in the area. Initial colonization of the Dutch John/Red Canyon area is indicated by the first appearance of *P. edulis* pollen c. 970 yr BP (Fig. 7). Establishment and population growth on the south face of Dutch John Mountain are marked by the first occurrence of macrofossils and the pollen increase 615 yr BP.

The Dutch John/Red Canyon region was colonized by *P. edulis* via long-distance seed dispersal. The minimum distance for this event (or events) was c. 40 km, assuming that the source populations were the nearest extant populations to the south. Once initial *P. edulis* populations were established, they expanded within a few centuries to cover a broad area (c. 5500 ha; Fig. 2) and elevational range (400 m).

DISCUSSION

Late Wisconsinan biogeography of montane conifers: comparing fossils and phylogeography

Forests and woodlands of the Central Rocky Mountains (comprising northern Colorado, north-eastern Utah, Wyoming, south-eastern Idaho and south-western Montana) occupy a wide elevational range, from subalpine forests bordering alpine tundra to low-montane and scarp woodlands bordering steppe and grasslands. Pre-Holocene biogeography of the constituent woody species of the region is obscure. Our results add to an emerging picture, however. Studies of woodrat middens and lake sediments to the south (Colorado Plateau and south-western

deserts) indicate that such low-montane species as *J. osteosperma*, *P. edulis* and *P. ponderosa* var. *scopulorum* were restricted to the south-western USA during the last glacial maximum, migrating northward 500–1000 km during the Holocene into the central Rockies, northern Great Basin and northern Colorado Plateau (Betancourt, 1990; Thompson, 1990; Van Devender, 1990a,b; Anderson, 1993; Weng & Jackson, 1999). Absence of these species from all glacial-age and late-glacial middens at Dutch John Mountain, and the delay of their appearance in the region until the Holocene, supports this inference (Betancourt *et al.*, 1991; Lyford *et al.*, 2003; J. Norris, S.T. Jackson & J.L. Betancourt, unpubl. data).

Pollen and macrofossil studies of lakes and peatlands in the Central Rockies are primarily from high-elevation landscapes that were glaciated before 16,000 yr BP. Whitlock (1993) summarizes circumstantial evidence from north-western Wyoming that populations of subalpine conifers (*Picea engelmannii*, *A. lasiocarpa*, *P. contorta*) persisted on the flanks of interior mountain ranges during the last glacial period. Rapid colonization of deglaciated landscapes in the Yellowstone-Teton region by *Picea* suggests that *P. engelmannii* populations must have occurred near the Yellowstone ice sheet (Whitlock, 1993). *Picea glauca* populations occur today on the flanks of the Yellowstone Plateau (Fertig & Jones, 1992) and in the Bighorn Mountains (S.T. Jackson, pers. obs.), so the initial colonizer may have been *P. glauca*. However, *A. lasiocarpa*, *P. contorta*, *P. albicaulis* established populations in the Yellowstone-Teton region and other mountain ranges during the late-glacial period, suggesting nearby Pleistocene populations (Baker, 1976, 1983; Whitlock, 1993).

None of the subalpine conifers of the central Rockies occur in the glacial-age and late-glacial middens at Dutch John Mountain. Their absence is surprising in view of the occurrence of *P. engelmannii* and *A. lasiocarpa* in late-glacial middens at Allen Canyon Cave (Betancourt, 1990), 350 km to the south and 100–200 m above Dutch John Mountain (Table 2; Fig. 1). These species also grew on the Kaibab Plateau of northern Arizona (2500–2800 m) during the late-glacial (Weng & Jackson, 1999) (Table 2, Fig. 1), and *P. engelmannii* occupied the Mogollon Rim of central Arizona (2222 m) during the last glacial maximum (Anderson, 1993). Absence of these species at Dutch John Mountain may indicate drier conditions in the central Rockies, which is consistent with the 10° southward displacement of the polar jet during the last glacial (Bartlein *et al.*, 1998). Paradoxically, a steep north-to-south increase in precipitation may have led to occurrence of subalpine conifers at higher elevations in the central Rockies than in the Colorado Plateau to the south. This conclusion remains tentative, however, until midden records are obtained from more mesic sites in the central Rockies.

Pinus contorta populations occur as low as 2400 m in the Uinta Mountains, so only a modest elevational displacement would have been required for this species to occupy slopes of Dutch John Mountain during the last glacial period. The scarcity of *Pinus* subgenus *Pinus* pollen in glacial and late-glacial middens (Fig. 7) suggests that *P. contorta* populations

Table 2 Previously published occurrences of mid-elevation and subalpine conifers from low to mid-elevation sites (≤ 2600 m) in the Colorado Plateau region, south of Dutch John Mountain

Site	Elevation (m)	<i>Pseudotsuga menziesii</i>	<i>Juniperus scopulorum</i>	<i>Pinus flexilis</i>	<i>Picea pungens</i>	<i>Picea engelmannii</i>	<i>Picea</i> sp.	<i>Abies lasiocarpa</i>	<i>Juniperus communis</i>	Citation
Chaco Canyon (22; 2)	1860–2020	11,790–11,170 (2)	11,790–11,170 (2)	11,790–11,170 (2)		11,170 (1)				Betancourt & Van Devender (1981)
Canyon de Chelly (2; 2)	1770	13,960 (1)	13,960 (1)	13,960 (1)	13,960 (1)					Betancourt & Davis (1984)
Eastern Grand Canyon (25; 13)	1600–2200	27,170–9540 (13)		27,170–14,120 (9)		27,170–14,120 (5)			27,170–14,120 (5)	Cole (1990)
Fracas Lake (31; 20)	2518				13,020–11,000 (3)	13,020–12,500 (2)	> 13,020–11,000 (12)	12,500 (1)		Weng & Jackson (1999)
Escalante River (10; 6)	1100–1300	14,110–13,680 (2)	12,720 (1)			14,110–14,070 (2)				Withers & Mead (1993)
Harmony Flat Shelter (2, 2)	1820	27,810–11,150 (2)	27,810–11,150 (2)	27,810–11,150 (2)		27,810–11,150 (2)			27,810–11,150 (2)	Mead <i>et al.</i> (1987)
Long Canyon Cave (7; 3)	1390				17,710 (1)					Betancourt (1990)
Bechan Cave (4, 4)	1310				13,690–15,530 (4)				13,690–15,530 (1)	Davis <i>et al.</i> (1984)
Cottonwood Cave (5; 4)	1390	18,700–14,100 (4)	15,330–14,100 (4)	18,700–14,100 (4)	18,700–14,610 (3)					Van Devender <i>et al.</i> (1984), Betancourt (1990)
Falling Arch (6; 3)	1460	23,350–15,750 (2)	23,350–15,750 (2)	23,350–15,750 (2)						Betancourt (1990)
Fishmouth Cave (8; 4)	1585	16,560–11,170 (4)	16,560–12,200 (3)	16,560–12,200 (3)	16,560–15,410 (2)				16,560–15,410 (2)	Betancourt (1984, 1990)
Allen Canyon Cave (9; 4)	2200	13,180–present (9)		13,180–10,180 (4)	13,180–10,870 (4)	13,180–10,870 (4)		13,180–10,870 (4)	3670 (6)	Betancourt (1984, 1990)
Cowboy Cave (1; 1)	1710	13,820 (1)				13,820 (1)				Spaulding & Van Devender (1977)
Bison Alcove (12, 8)	1317	23,750–14,350 (8)		23,750–14,350 (8)						Sharpe (1991)
Sand Canyon Alcove (4, 3)	1920	11,230–10,220 (2)	11,230–9490 (3)	11,230–9490 (3)	11,230–10,220 (2)				11,230–10,220 (2)	Sharpe (1991, 2002)

For each site, total number of midden or sediment samples are shown in parentheses, with total number of pre-Holocene samples in italics. Age ranges for each taxon at each site are shown; total number of occurrences for each taxon at the site are in parentheses. All dates are expressed in calendar-years before present.

Table 3 Plant macrofossil data not plotted in Figs 5 and 6

Genus/ family	Midden number (macrofossil relative abundance)
<i>Amaranthus</i> sp.	560 (2)
<i>Amelanchier utahensis</i>	572B/D (1)
<i>Artemisia</i> sp.	610 (1); 608 (2); 573 (2); 323 (2); 613B (2); 559 (1)
Asteraceae stems	325A (5); 609A (4); 325C (3); 322 (2); 572B/D (2); 607C (2); 607A (2); 607B (2)
Asteraceae achenes	325C (2); 322 (1); 572B/D (2); 325B (2); 607A (2); 607B (3); 326 (2); 574 (1); 616 (2); 559 (3)
cf. <i>Astragalus</i> sp.	570 (2)
<i>Atriplex</i> sp.	560 (2)
<i>Chenopodium</i> sp.	572 (3); 572A (2); 556A (2)
cf. <i>Crataegus</i> sp.	572B/D (2)
<i>Daucus/Cymopterus</i>	325A (2); 325C (2); 607A (1)
<i>Erodium</i> sp.	607B (2)
<i>Linum</i> sp.	609B (3)
<i>Mammillaria</i> sp.	322 (2); 572B/D (3)
cf. <i>Prunus</i> sp.	572B/D (1)
<i>Purshia tridentata</i>	559 (2)
cf. Scrophulariaceae	325A (2); 325C (2); 572B/D (2)
<i>Stipa comata</i>	321A (2); 555B (2); 303 (2)
<i>Stipa</i> sp.	572A (2); 622 (2)
<i>Trifolium</i> sp.	572B/D (2)

Middens are ordered from oldest to youngest.

Table 4 Pollen data not plotted in Fig. 7

Genus/family	Midden number (pollen percentage)
<i>Abies</i>	622 (0.2); 621 (0.3)
<i>Acer</i>	618A (0.2); 621 (0.3); 617 (0.2)
<i>Betula</i>	618A (0.2); 620 (0.3); 621 (0.3)
<i>Quercus</i>	618A (0.5); 615 (0.3); 622 (0.6)
<i>Ulmus</i>	622 (0.2)
<i>Alnus</i>	622 (0.2); 621 (0.3)
<i>Salix</i>	325C (0.3); 622 (0.4); 621 (0.3); 202B (0.3)
Rosaceae	325C (0.9); 618A (0.7); 615 (0.6); 620 (0.6); 621 (0.9); 559 (0.3)
Cactaceae	621 (0.3); 559 (0.3)
Caryophyllaceae	615 (0.3)
<i>Epilobium</i>	556 (0.3); 620 (0.3); 569 (0.3); 323 (0.3); 621 (0.3), 616 (0.6); 559 (0.3); 617 (0.2)
Liguliflorae	621 (0.3)
<i>Polygonum</i>	325C (0.3)
Apiaceae	325C (0.6); 616 (0.3)
<i>Urtica</i>	622 (0.2); 621 (0.3)

Middens are ordered from oldest to youngest.

were sparse throughout the region. *Pinus* subgenus *Pinus* pollen dominates pollen assemblages from lower treeline to the alpine zone in the central Rockies today (Whitlock, 1993; Lynch, 1996). Absence of *P. contorta* from Dutch John Mountain, and absence or scarcity in the surrounding region,

may be attributable to low precipitation. Significantly, *Pinus* subgenus *Pinus* pollen is poorly represented in lake-sediment records throughout the central Rockies before c. 11,000 yr BP (Davis *et al.*, 1986; Barnosky *et al.*, 1987; Whitlock, 1993; Lynch, 1998). Most pre-Holocene *Pinus* pollen is *Pinus* subgenus *Strobus* (i.e. *P. flexilis* and/or *P. albicaulis*).

The pre-Holocene whereabouts of montane tree species (*Pseudotsuga menziesii*, *P. flexilis*, *Picea pungens*, *J. scopulorum*), which grow today below the subalpine forests but above or intermixed with lower-treeline species, are poorly known in the central Rockies. Pollen and macrofossils of *Pseudotsuga* typically do not occur in montane/subalpine lake sediments in the central Rockies until after 11,000 yr BP (Mehring *et al.*, 1977; Baker, 1983; Whitlock, 1993), which could indicate either climate-mediated upslope expansion from local Pleistocene populations, or climate- or dispersal-mediated delays in migration from regions to the south. All four species occur in glacial-age and late-glacial macrofossil assemblages from the southern Colorado Plateau (Table 2), and all are represented in late-glacial woodrat middens (c. 11,225 yr BP) at Sand Canyon Alcove in north-western Colorado, 65 km SE of our study site (Sharpe, 1991, 2002).

Our study indicates that populations of *Pseudotsuga menziesii*, *P. flexilis* and *Picea pungens* grew on the south slopes of Dutch John Mountain during the last glacial period, together with *J. communis* (Fig. 5). *Juniperus scopulorum* populations occurred there by 18,780 yr BP. These species were joined by *J. horizontalis* 11,110 yr BP (Fig. 5), and all persisted at the site until at least 10,235 yr BP. Assemblages consisting of all of these species except *J. horizontalis* are documented from several sites in the southern Colorado Plateau region, spanning a broad elevational range (1300–2200 m) (Table 2). Occurrence of these species at Dutch John Mountain (2050 m) and Sand Canyon Alcove (1920 m) (Sharpe, 1991, 2002), c. 400 km north of the southern Colorado Plateau sites, suggests a broad band of woodlands or forests dominated by montane conifers (*Pseudotsuga*, *P. flexilis*, *Picea pungens*, *J. communis*, *J. scopulorum*) extending from the Grand Canyon region to southern Wyoming during the last glacial period. Much of the Colorado Plateau landscape currently occupied by pinyon–juniper woodlands may have been vegetated by these montane conifer forests or woodlands.

Biogeographers and geneticists have often assumed that geographical ranges of western coniferous species were highly fragmented during the last glacial period, as witnessed by the emphasis on identifying ‘glacial refugia’ for these species. Palaeoecological evidence indicates a more complicated picture. Some species were more fragmented today, while others were more extensive and highly connected. The montane conifers of the Colorado Plateau region represent a case in point. These species, and presumably many of their understory, animal and fungal associates, had extensive, probably continuous ranges during the last glacial period, although some of them may have been more highly fragmented (or absent) in regions to the north. We discuss the implications of

the glacial-age occurrences of these species at Dutch John Mountain and sites to the south in the context of modern genetic and distributional data.

Pseudotsuga menziesii

Studies from the Great Basin suggest that *Pseudotsuga menziesii* was displaced far south of its present range during the last glacial maximum, expanding northward into east-central Nevada and south-western Utah in the late-glacial (Wells, 1983b; Thompson, 1990). Tsukada (1982) suggested from pollen evidence that *Pseudotsuga* populations in the Pacific Northwest derived from migration of populations from glacial refugia far to the south, in the southern Rockies. In contrast, studies to the east show that *Pseudotsuga* populations occurred much further north, in the Grand Canyon (Cole, 1990) and Canyonlands regions (Sharpe, 1991) (Table 2), and our study indicates that *Pseudotsuga* occurred in the northern Colorado Plateau/central Rockies region during the last glacial maximum (Fig. 5). Hence, modern montane populations in these regions probably derived from upslope migration of Wisconsinan populations during the late-glacial and early Holocene.

Pseudotsuga populations throughout the Great Basin, Colorado Plateau and central Rockies show high genetic diversity (Li & Adams, 1989; Schnabel *et al.*, 1993). In the Colorado Plateau and central Rockies, this diversity likely derives directly from conservation of genetic diversity within local populations throughout at least the last glacial/interglacial cycle; genetic diversity within conifer species tends to be concentrated within rather than among populations (Hamrick & Godt, 1989). However, allozyme studies indicate strong differentiation among populations within the Rockies. Distinct groups occur in the north-central and northern Rockies and the south-central and southern Rockies, with the boundary running through southern Idaho and central Wyoming (Li & Adams, 1989). Within the southern group, populations in western Wyoming and south-eastern Idaho differ markedly from those in Utah and Colorado. Li & Adams (1989) proposed that modern *Pseudotsuga* populations in Wyoming and south-eastern Idaho originated from local glacial-age populations, and not from northward migration. Our demonstration of glacial-age *Pseudotsuga* populations on the flanks of the Uintas is consistent with that scenario, but studies from Wyoming and Idaho are clearly needed.

Pinus flexilis

Our records of glacial-age *P. flexilis* from Dutch John Mountain fit an emerging pattern in which *P. flexilis* was widely distributed in scarps, foothills, and flanks of mountain ranges and plateaus throughout the Great Basin (Wells, 1983b; Thompson, 1990), Colorado Plateau (Table 2), western Great Plains (Wells, 1983a; Wells & Stewart, 1987a,b), and southern and central Rockies (this study). It grew at least as far north as Bighorn Canyon on

the Wyoming/Montana border (J.L. Betancourt, S.T. Jackson & M.E. Lyford, unpubl. data).

Two recent studies have revealed regional patterns of genetic diversity in *P. flexilis*, one based on mitochondrial DNA (Mitton *et al.*, 2000) and the other on allozymes (Jørgensen *et al.*, 2002). Mitton *et al.* (2000) identified eight haplotypes, some with restricted ranges and others more widespread. Jørgensen *et al.* (2002) observed that populations from the Northern Rockies (Canada, Montana) were genetically similar to those from the Colorado Front Range, that populations from the Great Basin (Nevada, California) showed high genetic variation among sites, and that populations from the northern Colorado Plateau and interior central Rockies (Utah, Idaho) were genetically closer to the Great Basin populations than the Northern Rockies and Front Range groups.

Mitton *et al.* (2000) interpreted the haplotype patterns as deriving from various 'refugia' occupied by *P. flexilis* populations during the last glacial period. Jørgensen *et al.* (2002) suggested a more complex origin, invoking glacial isolation for some populations but noting correctly that *P. flexilis* populations were widespread in the Great Basin and Great Plains-Rocky Mountains border region during the last glacial period. Evidence summarized in our paper indicates that *P. flexilis* was also widespread and well-connected in the Colorado Plateau region, from the Grand Canyon to the flanks of the Uintas (see Table 2). Jørgensen *et al.* (2002) proposed that the haplotype patterns observed by Mitton *et al.* (2000) were attributable to isolation in earlier glacial periods. However, we see no reason to conclude that the pattern of glacial expansion/coalescence and interglacial contraction/isolation of *P. flexilis* populations observed in the last glacial-interglacial cycle is not characteristic of earlier cycles. The earth system has experienced five interglacial periods during the past half-million years, and *P. flexilis* populations may have experienced contractions and isolation events during each of these. In particular, the previous (Sangamonian or Stage 5) interglacial period was warmer in many regions than the current (Holocene) interglacial; *P. ponderosa* grew on the Yellowstone Plateau (Baker, 1986), which it has never occupied during the Holocene (Whitlock, 1993). Although some haplotypes may have originated during the last glacial period (Mitton *et al.*, 2000) or earlier glacial periods (Jørgensen *et al.*, 2002), we regard haplotype differentiation during the Sangamonian and previous interglacials as a viable explanation for the phylogeographical patterns.

Juniperus scopulorum

Juniperus scopulorum occurs in montane woodlands throughout the Rockies, extending north into central British Columbia (Little, 1971; Noble, 1990). During the last glacial maximum, it had a wide distribution, ranging from southern Arizona (Van Devender, 1990b), New Mexico (Betancourt *et al.*, 2001; Holmgren *et al.*, 2003), and west Texas (Van Devender, 1990a) to the southern Colorado Plateau (Betancourt, 1990) and Great Basin (Thompson, 1990). It is absent from most glacial-age middens in the northern Colorado Plateau and

Great Basin regions, however (Table 2) (Wells, 1983b; Thompson, 1990). Although it is absent from the oldest Dutch John Mountain middens, it occurred there at least by 18,730 yr BP.

Chemosystematic studies suggest that *J. scopulorum* populations in the central and northern Rockies derived from post-glacial migration of glacial-age populations that grew in the southern Rockies and Colorado Plateau regions (Adams, 1983). The fossil record generally supports this hypothesis. *Juniperus scopulorum* may have expanded northward in response to warming after the last glacial maximum 21,500 yr BP, arriving at Dutch John Mountain by 18,780 yr BP. It reached the Wyoming/Montana border no later than 11,320 yr BP (Lyford *et al.*, 2002).

Picea pungens

Picea pungens occurred infrequently in glacial-age middens, and was more abundantly and consistently represented in late-glacial middens (12,740–10,610 yr BP). Late-glacial populations are recorded to the south in southern Utah, northern New Mexico, and northern Arizona (Table 2). *Picea pungens* occurs in middens dating from 27,560 to 28,670 yr BP at southern Bighorn Canyon (J.L. Betancourt, S.T. Jackson & M.E. Lyford, unpubl. data), 450 km north of Dutch John Mountain and 230 km NE of the modern northern range limits of the species. *Picea pungens* evidently occurred farther north and east during the last glacial period.

Studies of genetic variability in *Picea pungens* suggest differences between northern (Wyoming, Colorado, Utah) and southern (Arizona, New Mexico) populations (Hanover, 1974; Bongarten & Hanover, 1986a,b). The scattered palaeoecological data indicate that the northern populations were not displaced to the south during glacial periods. *Picea pungens* is documented in late-glacial middens in southern New Mexico/western Texas (Van Devender, 1990a). This, together with the late-glacial populations documented in the Colorado Plateau and central Rockies and the glacial-age occurrence at Bighorn Canyon, indicates that *Picea pungens* had a broader glacial and late-glacial distribution than today, extending from 32° N to at least 45° N. A possible disjunct population near the Montana/Alberta border (Strong, 1978) may indicate an even broader distribution. North–south differentiation in *Picea pungens* may not be attributable to glacial isolation. Today, southern populations are smaller and more isolated than northern populations (Little, 1971), and hence the differentiation may be a product of interglacial isolation.

Juniperus horizontalis

Juniperus horizontalis is widely distributed in boreal North America, with a few scattered, isolated populations in the northern Great Plains and central Rockies. In the latter regions it hybridizes extensively with *J. scopulorum* (Adams, 1983). It occurred on Dutch John Mountain from 11,815 to 6710 yr BP (Fig. 5). The nearest extant populations of this species are in the Rattlesnake Hills of central Wyoming and the Laramie Range of

south-eastern Wyoming (<http://www.rmh.uwyo.edu>), respectively, 275 and 340 km from Dutch John Mountain. Populations of *J. horizontalis* are widespread in northern Wyoming, occurring on the flanks of the Absaroka, Owl Creek, and Bighorn Mountains and the Black Hills. Our data suggest that glacial-age populations occurred near the flanks of the Uintas and expanded onto slopes of Dutch John Mountain in the late-glacial, where they persisted until mid-Holocene extirpation (probably related to increasing temperatures and drought). Populations near and south of the Uintas may have given rise to the scattered isolates in the Bighorn Basin and elsewhere in the central Rockies and northern Plains, although glacial-age populations may have occurred locally in those regions as well.

Stasis and change at Dutch John Mountain: climate change, invasion and extinction

The major vegetational changes recorded at Dutch John Mountain during the past 40,000 years were driven ultimately by climatic change. Both of the major transitions – from floristically depauperate conifer woodlands of the full-glacial to rich, mesic conifer woodlands of the late-glacial between 18,000 and 14,000 yr BP, and from diverse, mesic conifer woodlands to relatively xeric Utah-juniper woodlands between 10,200 and 9500 yr BP – occurred during periods of well-documented climate change in the western interior of North America. The third, more-subtle transition, from Utah-juniper woodlands to pinyon–juniper woodlands between 1000 and 600 yr BP, also occurred during an important climatic transition.

Palaeoclimatic and palaeoecological records over much of the Northern Hemisphere indicate steady warming after 15,000 yr BP. Increasing precipitation during the late-glacial transition is recorded widely in the western interior of North America (Thompson *et al.*, 1993), coinciding with the northward shift of the polar jet stream as the continental ice sheets retreated (Bartlein *et al.*, 1998). Lake levels in the Bonneville Basin, 200 km to the west, and the Lahontan Basin, 700 km west, were highest during the late-glacial period (Oviatt, 1997; Benson, 2004).

Continued (and presumably gradual) warming, accompanied by drying, is recorded widely in the Colorado Plateau and central Rockies after 11,700 yr BP. At Fracas Lake (2520 m) on the Kaibab Plateau of northern Arizona, *P. ponderosa* invaded and replaced *Picea*-dominated forest 11,000 yr BP (Weng & Jackson, 1999). By 9725 yr BP, *P. ponderosa* expanded upward to Bear Lake at 2780 m, and montane *Picea pungens* replaced subalpine *P. engelmannii* as the dominant spruce on the Plateau (Weng & Jackson, 1999). *Pinus ponderosa* expanded on the Markagunt Plateau (> 2500 m) of south-western Utah c. 9500 yr BP (Anderson *et al.*, 1999), while populations of mesic and montane/subalpine species were extirpated at low elevations (1100–2200 m) in southern Utah and northern Arizona between 11,000 and 8500 yr BP (Betancourt, 1984, 1990; Cole, 1990; Withers & Mead, 1993).

Vegetational transitions are also recorded in the central Rockies during this interval. *Pinus contorta*-dominated forests

were established on the deglaciated Yellowstone Plateau by c. 10,500 yr BP (Whitlock, 1993), and mid-elevation (2750 m) *P. albicaulis/Picea/Abies* parklands in the Wind River Mountains were replaced by *P. contorta* parkland c. 9500 yr BP (Lynch, 1998). *Juniperus communis* populations disappeared between 10,000 and 8500 yr BP at low-elevation sites at Big Pryor Mountain in south-central Montana (Lyford *et al.*, 2002).

The differences in timing of late-glacial and early Holocene vegetational transitions across the Colorado Plateau and central Rockies may be attributable to gradual, time-transgressive climatic change together with differences in climatic thresholds for incumbent and invading species (Jackson & Overpeck, 2000). In a period of warming and drying, species adapted to warm and dry climates may be expected to invade southern and lower sites before northern and higher sites. Furthermore, critical temperature and/or moisture thresholds may differ between (for example) *P. ponderosa* and *P. contorta* that are invading subalpine *Picea/Abies* forests in different regions and elevations. Thus, the critical threshold for *P. contorta* expansion may have been passed at a different time in Wyoming than that for *P. ponderosa* in Arizona. The palaeoecological data available for the Colorado Plateau and central Rockies are consistent with gradual, Milankovitch-driven climatic changes postulated for the late-glacial/Holocene transition (Thompson *et al.*, 1993; Whitlock, 1993; Bartlein *et al.*, 1998).

The final major transition at Dutch John Mountain, the invasion of *P. edulis*, occurred during an apparent climate regime-shift, centred around 800 yr BP, which is recorded over much of North America (Bradbury & Dean, 1993; Ely *et al.*, 1993; Grissino-Mayer, 1996; Laird *et al.*, 1996, 2003; Schaffler & Jacobson, 2002; Booth & Jackson, 2003). Whether and how this transition was manifested in the study region is not clear. However, range expansion of *J. osteosperma* in northern Wyoming ceased between 1000 and 800 yr BP (Lyford *et al.*, 2003), and *P. ponderosa* expanded on the western (dry) slope of the Bighorn Mountains and in central Montana at that time (J. Norris, S.T. Jackson & J.L. Betancourt, unpubl. data). This may represent increased effective growing-season moisture in the region, which might also have facilitated *P. edulis* colonization at Dutch John Mountain. Decadal-scale climate variability may have played a defining role in the *P. edulis* expansion (Gray, 2003).

We cannot rule out the possibility that absence of *P. edulis* before 1000 yr BP resulted from dispersal limitations. *Pinus edulis* seeds are large, wingless and bird-dispersed (primarily corvids – pinyon jays, nutcrackers, etc.) (Chambers *et al.*, 1999). Although most corvids cache seeds within a few tens of metres of source trees, caches involving longer flights (up to 10 km) have been documented (Vander Wall & Balda 1981). Pinyon seeds were a favoured food of prehistoric peoples, who may have been effective agents of dispersal through long-distance trade of valued bumper crops (Mehring, 1986; Betancourt *et al.*, 1993). *Pinus edulis* established populations at Owl Canyon in north-central Colorado sometime between 1300 and 500 years ago, involving a dispersal event spanning at least 200 km (Betancourt *et al.*, 1991). *Juniperus osteosperma*, a

large-seeded species that may not be bird-dispersed (Schupp *et al.*, 1996; Chambers *et al.*, 1999), migrated rapidly from southern to northern Utah during the late-glacial, and made several dispersal jumps of 30–100 km in its Holocene invasion of Wyoming (Lyford *et al.*, 2002, 2003). Such long-distance dispersal events appear to be routine in post-glacial plant migrations (Clark *et al.*, 1998, 2001), so dispersal may not have been limiting to *P. edulis*. Nevertheless, rapid growth and expansion of human populations on the Colorado Plateau c. 1000 years ago (Dean, 1996) might have amplified the probabilities of long-distance seed dispersal along pinyon's periphery. Increased rates of long-distance dispersal could have interacted with low-frequency climate variability to increase the chances of pinyon colonization and expansion.

Not all climate transitions in the region were accompanied by changes in the Dutch John Mountain midden series. The abrupt Younger Dryas Interval (13,000–11,700 yr BP) was manifested in many parts of the Northern Hemisphere by severely depressed temperatures (Alley, 2000; National Research Council, 2002), and had substantial vegetational effects in eastern North America (Shuman *et al.*, 2002) and possibly Alaska (Hu *et al.*, 2002). The Younger Dryas is not well-documented in the interior western USA, although it has been associated with a rebound in ground-water and lake levels (e.g. Quade *et al.*, 1998; Polyak *et al.*, 2004), and Weng & Jackson (1999) suggest it may have influenced vegetational changes in northern Arizona. Our late-glacial midden series spans the Younger Dryas, but shows no clear responses (Fig. 5).

The midden series also shows relative stasis during most of the Holocene, between c. 7500 and 1000 yr BP (Figs 5–7). Important regional climatic transitions centred around 5400 and 2800 yr BP (summarized in Lyford *et al.*, 2002, 2003) were not accompanied by changes in midden assemblages. Furthermore, the woody components of the vegetation show greater turnover during the major transitions than the non-woody (herb, graminoid, cactus, low shrub) components (Figs 5 & 6). Many understory species have persisted since the late-glacial period (*Artemisia nova*, *Chrysothamnus viscidiflorus*, *Lithospermum*, *Opuntia*, *Lappula redowskii*), and some date to the last glacial maximum (*Oryzopsis*, *Krasscheninnikovia lanata*, *Gutierrezia sarothrae*) (Fig. 6). Of the canopy and subcanopy species, only *J. scopulorum* dates to the last glacial maximum (and only to the late phase), and *Rhus trilobata*, *Symphoricarpos*, *C. montanus*, and *C. ledifolius* var. *intricatus* to the late-glacial (Fig. 5).

Interpretation of patterns in the fossil record requires careful consideration of what aspects of past populations and communities are recorded by fossil assemblages. Macrofossil assemblages from fossil woodrat middens generally record presence/absence of species more reliably than absolute or relative abundance of species in surrounding vegetation (Dial & Czaplewski, 1990; Spaulding *et al.*, 1990; Lyford, 2001; Lyford *et al.*, 2004). Accordingly, vegetation at Dutch John Mountain may well have responded to late-glacial and Holocene climatic changes by altering density, biomass and relative abundance of species. Such changes would be masked by the midden assemblages, as long as floristic composition of

the vegetation remained constant. The dynamics recorded in the midden assemblages are primarily local invasion and extinction, and hence only climatic changes sufficient to extirpate an incumbent species or facilitate colonization of a new species would be reflected in the midden record.

Dynamics of local extinctions differ in important ways from dynamics of invasion and colonization. Invasion of a species requires a combination of suitable microenvironments and availability of propagules, and invading species face competition from incumbent populations. Invasion may be delayed or interrupted by periods of unfavourable climate, low propagule flux density, and absence of disturbances that create local opportunities for establishment (Davis, 1981; Woods & Davis, 1989; Clark *et al.*, 1998; Jackson & Booth, 2002; Booth *et al.*, 2004; Lyford *et al.*, 2003). In contrast, incumbent populations are typically resistant to elimination: locally adapted populations are established in place, propagule flux density is high, and, in many cases, microenvironments and disturbance regimes suitable for regeneration are maintained. Extinction of an incumbent population can come when the environment changes sufficiently to approach or exceed the environmental tolerances of the species or population, particularly if accompanied by invasion of new species better suited to the new environment.

Invasion/extinction dynamics may play out primarily in the juvenile phase. Adults of many woody plant species have broader environmental tolerances than their seedlings and juveniles, and hence extinction may proceed from reduction or cessation of recruitment followed by senescence of existing adults. This process may take place gradually, with populations initially disappearing from all but the most favourable sites, and ultimate elimination from the latter by stochastic processes (which might include climate variability). Particular climatic changes may or may not be accompanied by invasions and extinctions, depending on the nature, magnitude and rate of the climate change relative to the fundamental niches of the incumbents and potential invaders (Jackson & Overpeck, 2000), and whether suitable invaders are in position to disperse propagules to a site.

The patterns in the Dutch John Mountain midden records represent invasion/extinction dynamics at multiple scales, ranging from local to regional. Local dynamics include the appearance and subsequent disappearance from the midden record of such mesic plants as *Rosa*, *Rubus*, *Holodiscus dumosa*, *Philadelphus microphyllus* and *Artemisia ludoviciana*. All of these taxa are absent from full-glacial middens, abundant in late-glacial middens, and absent from Holocene middens (Figs 5 & 6). All grow locally on Dutch John Mountain today. Their late-glacial appearance may represent immigration from distant sources or expansion from local sources as climate became warmer and wetter. Their disappearance in the late-glacial/Holocene transition represents contraction of widespread populations to mesic microsites (shaded ravines, gulches, drainages) as climate became warmer and drier. The early Holocene disappearance of *P. flexilis* and *Pseudotsuga menziesii* from the midden record (Fig. 5) is also attributable to extirpa-

tion from all but the most mesic local habitats. These species occur in deep canyons along the Green River below Dutch John Mountain, and a few individuals of *Pseudotsuga* grow on the north slope of Dutch John Mountain. One individual of *Pseudotsuga* grew in a relatively moist ravine on the south slope until the 2002 fire. The *Pseudotsuga* populations may not have existed continuously during the Holocene, however. A source-sink dynamic may have developed, with periodic recolonization from sources in Red Canyon or elsewhere.

All of the past constituents of the Dutch John Mountain flora persist in populations within 10–20 km of the site today, with one exception. *Juniperus horizontalis* has undergone universal extinction in the Uinta Mountain/Green River region. It persists in scattered populations in Wyoming and Montana, which date to the late-glacial (Lyford *et al.*, 2002) and possibly earlier.

Several species, including *J. osteosperma*, *C. ledifolius* var. *intricatus*, *C. montanus*, *P. ponderosa*, *P. edulis*, and *Ephedra viridis*, represent net additions to the flora of Dutch John Mountain in the last 13,000 years. All of these species are well-represented in modern middens, even when sparse in local vegetation (Lyford *et al.*, 2004), so their absence from glacial-age and early late-glacial middens at Dutch John Mountain and other sites in the Colorado Plateau region indicates they migrated from the south. Dutch John Mountain, as well as the surrounding region, has accumulated woody plant species since the last glacial maximum.

A number of xeric-adapted low shrubs and non-woody species persisted in the record during the past 13,500–40,000 years (*Oryzopsis*, *Krasscheninnikovia lanata*, *Cryptantha*, *Gutierrezia sarothrae*, *Artemisia nova*, *Chrysothamnus viscidiflorus*, *Lithospermum*, *Opuntia*, *Lappula redowskii*) (Fig. 6). Together with *J. scopulorum*, this group does not display the extinction/invasion dynamics of most woody species and more-mesic non-woody plants (e.g. *Artemisia ludoviciana*, *Carex*). Long-term persistence of xeric plants is well-documented in other midden series from western North America (Betancourt, 1990; Spaulding, 1990; Thompson, 1990; Van Devender, 1990a,b; Nowak *et al.*, 1994; Betancourt *et al.*, 2001; Lyford *et al.*, 2002), although the species differ from region to region. Such species may have broad niches or high genetic variability, allowing them to maintain local populations despite substantial climate change. However, the contrast at Dutch John Mountain between the persistent xeric taxa and the mesic late-glacial taxa suggests an alternative explanation. Open, xeric habitats may have always been present in high density on the steep, south-facing slopes of Dutch John Mountain (Fig. 3), in spite of substantial changes in temperature and precipitation since the last glacial maximum. Any given midden site on these slopes would always be within a few metres of locally xeric habitats, regardless of the macroclimatic regime. In contrast, mesic habitats are more widely scattered today. During the cooler, wetter late-glacial interval, these habitats occurred at higher density on the south-facing slope, increasing the likelihood that populations of mesic plants would be in the vicinity of any given midden site.

CONCLUSIONS

Analyses of plant macrofossils from woodrat middens at Dutch John Mountain provide a detailed, 40,000-year record of climatic and vegetational change in a poorly known part of the western North American interior. Glacial-age and late-glacial assemblages at the site add to an emerging pattern in which conifer woodlands consisting of *P. flexilis*, *Pseudotsuga menziesii*, *Picea pungens*, *J. communis* and *J. scopulorum* covered extensive regions of the Colorado Plateau, from the Grand Canyon to the Utah/Wyoming border. Their occurrence at Dutch John Mountain is somewhat surprising in view of its northerly location and high elevation relative to Colorado Plateau sites. Sites of comparable elevation and identical bedrock to the south were occupied by subalpine conifers (*Picea engelmannii*, *A. lasiocarpa*). This vegetational pattern is consistent with a northward decrease in precipitation in the region owing to southward displacement of the polar jet stream, but the relatively xeric, south-facing slopes of Dutch John Mountain may also have played a role.

Mesic conifer woodlands persisted at Dutch John Mountain through the late-glacial. Rich, diverse subcanopy and understory vegetation indicates that conditions were moister during the late-glacial than the full-glacial period. The mesic vegetation gave way rapidly during the early Holocene to xeric woodlands dominated by *J. osteosperma* with scattered *J. scopulorum* and *P. ponderosa*. These woodlands persisted relatively unchanged until the invasion of *P. edulis*, which commenced *c.* 800 yr BP. The *P. edulis* invasion is associated with a climatic regime-shift in the region, although it may have been facilitated or accelerated by long-distance seed dispersal by humans or birds.

Overall, the Dutch John Mountain midden record, like others in the western North American interior, shows patterns of invasion, persistence and extinction tied to climatic changes of the past 40,000 years. Dutch John Mountain has generally accumulated plant species since the last glacial maximum, although many species, especially mesic species, are relatively restricted today. Some species (e.g. *Pseudotsuga menziesii*) may be maintained by periodic recolonization from distant source populations during wet climatic intervals. Three species of the full- and late-glacial periods (*P. flexilis*, *J. communis*, *Picea pungens*) have disappeared completely from Dutch John Mountain, but persist at higher elevations and/or in canyons within a few kilometres. Only one species, *J. horizontalis*, has undergone regional extinction. The dominant species on the slopes today, *J. osteosperma*, and *P. edulis*, are Holocene adventives, as are *P. ponderosa* and *Ephedra viridis*.

ACKNOWLEDGEMENTS

Invaluable assistance in field and laboratory was provided by Gabe Cisneros, Mark Betancourt, Jodi Norris, Camille Holmgren, Robert Gillis, Chris van Kirk, Kate Rylander and Rob Eddy. We thank Sherel Goodrich of the Ashley National

Forest for providing data and information on vegetation and flora of the Dutch John Mountain region. This research was supported by grants to the University of Wyoming and the University of Arizona from the National Science Foundation (Ecology and Palaeoclimate Programmes), and by the US Geological Survey.

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BIOSKETCHES

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Editor: Philip Stott