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INFLUENCE OF LANDSCAPE STRUCTURE AND CLIMATE VARIABILITY ON A LATE HOLOCENE PLANT MIGRATION

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Abstract. We analyzed and radiocarbon-dated 205 fossil woodrat middens from 14 sites in central and northern Wyoming and adjacent Utah and Montana to document spatiotemporal patterns of Holocene invasion by Utah juniper (*Juniperus osteosperma*). Holocene migration into central and northern Wyoming and southern Montana from the south proceeded by a series of long-distance dispersal events, which were paced by climate variability and structured by the geographic distribution and connectivity of suitable habitats on the landscape. The migration of Utah juniper into the region involved multiple long-distance dispersal events, ranging from 30 to 135 km. One of the earliest established populations, on East Pryor Mountain in south central Montana, is currently the northernmost population of the species. Establishment by long-distance dispersal of that population and another in the Bighorn Basin occurred during a period of relatively dry climate between 7500 and 5400 years ago. Further expansion of these initial colonizing populations and backfilling to occupy suitable sites to the south was delayed during a wet period from 5400 to 2800 years ago. Development of dry conditions 2800 years ago led to a rapid expansion in which Utah juniper colonized sites throughout its current range. Landscape structure and climate variability play important roles in governing the pattern and pace of natural invasions and deserve close attention in studying and modeling plant invasions, whether exotic or natural.

Key words: climate variability; Juniperus osteosperma; *landscape structure; long-distance dispersal; Utah juniper; woodrat middens.*

Introduction

Biological invasions have become a central concern for ecologists and conservation biologists. Invasions of nonindigenous species, set into motion by accidental or deliberate intercontinental introductions by humans, are threatening native communities and global-scale biodiversity (Elton 1958, Carlton 1996, Vitousek et al. 1996, Stohlgren et al. 1999, Mack et al. 2000, Mooney and Hobbs 2000, Richardson et al. 2000, Rosenzweig 2001). Natural invasions, the expansion of native species into new regions or habitats in response to environmental change, are also driving changes in community structure and ecosystem biogeochemistry (Hobbs and Mooney 1986, Davis et al. 1992, Padien and Lajtha 1992, Archer et al. 2001, Hibbard et al. 2001).

Ecologists are devoting considerable effort to understanding and modeling the mechanisms underlying biological invasions (Higgins and Richardson 1996, Shigesada and Kawasaki 1997, 2002, Ronce 2001, Keane and Crawley 2002, Nathan et al. 2002, Shea and Chesson 2002). These efforts have tended to emphasize biological processes of dispersal, establishment, population growth, and competition against a more or less uniform environmental backdrop. The role of environmental heterogeneity is generally acknowledged, but is frequently ignored or treated as a binary classification of suitable and unsuitable sites in modeling efforts (Shigesada and Kawasaki 1997, 2002). However, landscape structure—the spatial distribution of habitats and resources—can have a strong effect on the course of invasions (With 2002). Furthermore, temporal variability in the environment is often ignored or modeled as stochastic variation about a constant mean (Mack 1995). Climatic variability, however, is typically nonstationary (Swetnam and Betancourt 1998, Gray et al. 2003), and interacts with landscape structure. Sites unfavorable or marginal for population establishment under one climatic regime may become highly suitable under another, and vice versa. Environmental variability at annual to millennial time scales must be considered in assessing likelihood of colonization and spread of natural populations as well as introduced species.

Natural invasions have occurred routinely in the past in response to long-term environmental change (Webb 1987, Huntley and Webb 1988, Swetnam et al. 1999, Jackson and Overpeck 2000), and can be expected to become more prevalent in coming decades in response to human land-use and global change (Parmesan et al. 1999, Walther et al. 2002). Past natural invasions can serve as model systems for understanding ongoing and future natural invasions, as well as for studying how

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landscape structure and climatic variability influence both alien and natural invasions over time scales of 100–10 000 yr. Analysis of past invasions using historical and paleoecological data can reveal patterns and processes unseen in studies of invasions that span only the past few decades (Huntley et al. 1997, Jackson 1997, Pitelka et al. 1997, Clark et al. 1998, Davis et al. 1998, Swetnam et al. 1999). Furthermore, ongoing natural invasions may be inadequately understood in the absence of knowledge about past invasion patterns. For instance, woodland expansions attributed to human land-use practices (grazing, fire suppression) may in some cases represent continuation or resumption of invasions initiated long before Euro-American settlement (Swetnam et al. 1999).

Paleoecological studies of plant invasions require spatial networks of time-series data that record local establishment and expansion of populations (Clark et al. 1998). Pollen sequences from lake and wetland sediments provide time-series of vegetational changes, but are frequently limited in taxonomic precision, owing to inability to discriminate species within most genera (and genera within many families). Furthermore, pollen sequences are generally ineffective at discriminating between presence of small, local populations and distant regional ones (Bennett 1985, Davis et al. 1991, MacDonald 1993). Pollen data are often blind to isolated pioneer populations unless those populations occur near very small basins (Parshall 2002).

In contrast to pollen data, plant macrofossils provide greater taxonomic precision (most can be identified to species), as well as greater spatial precision (~10–100 m). Time series of plant macrofossil data from lake sediments have provided detailed spatiotemporal records of plant invasions at spatial scales ranging from regional (e.g., Jackson and Booth 2002) to subcontinental (Jackson et al. 1997). Fossil middens collected by woodrats (*Neotoma*) are ubiquitous in the canyons and bedrock escarpments common throughout the arid and semiarid western United States (Betancourt et al. 1990). The middens contain abundant, well-preserved, plant organs that the woodrats habitually collect from within 10–100 m of the midden site (Finley 1958, 1990; Lyford et al., *in press*). Midden deposition is episodic, and hence each midden represents a snapshot in time. Individual fossil middens within a single canyon or bedrock exposure may vary widely in age, and so multiple radiocarbon-dated middens can be stacked to provide a time-series of plant macrofossil data for a single area (canyon or escarpment) within a restricted elevational range. Several recent studies have shown the utility of time series of midden-macrofossil data for inferring the timing of local plant invasions at single sites (Betancourt et al. 1991, 2001, Nowak et al. 1994, Jackson et al. 2002, Lyford et al. 2002). Spatial and temporal patterns of past natural invasions can be documented by employing a spatial array of midden series (Lanner and Van Devender 1998, Hunter et al. 2001), analogous to synoptic-scale summaries of pollen and plant macrofossil data from lake sediments (Webb 1988, Jackson et al. 1997, Williams et al. 2001). Synoptic midden studies are ideal for tracking the migration of widely distributed taxa with persistent macrofossils, such as the numerous juniper, pine, and pinyon species that dominate vegetation of rocky habitats across western North America.

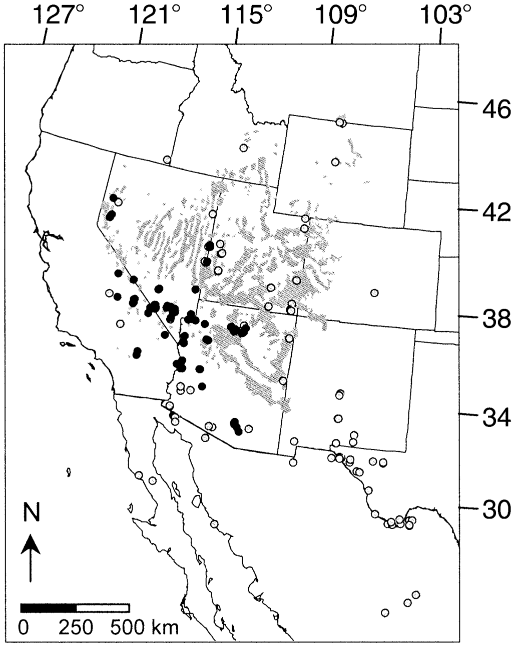

FIG. 1. Map of Utah juniper distribution in western North America (Little 1971), with records of presence (filled circles) and absence (open circles) of Utah juniper macrofossils in 415 woodrat middens dating between 40 and 13 ka (from compilation of published and unpublished sources).

The geographic distribution and biogeographic history of Utah juniper (*Juniperus osteosperma*), a coniferous, evergreen woodland shrub, suggests that it migrated into the northern part of its current range with postglacial warming and drying (i.e., within the past 10 000 years; Fig. 1). The species distribution consists of a core of extensive, closely spaced populations in the Great Basin and Colorado Plateau regions, and a series of widely scattered satellite populations in the central Rocky Mountain regions of eastern Idaho, western and central Wyoming, and adjacent Montana (Fig. 1). Woodrat-midden evidence indicates that Utah juniper was limited to the southern Great Basin and northern Mohave and Sonoran Desert regions during the last glacial maximum and late-glacial transition (40–13 ka [thousands of years ago]) (Fig. 1). During the last glacial period, lowlands in northeastern Utah, central Wyoming, and southern Montana harbored higher-elevation species such as *Pinus flexilis*, *Picea pungens*, *Pseudotsuga menziesii*, and *Juniperus communis* (Sharpe 1991, 2002, Lyford et al. 2002; J. L. Betancourt, S. T. Jackson, and M. E. Lyford, *unpub-*

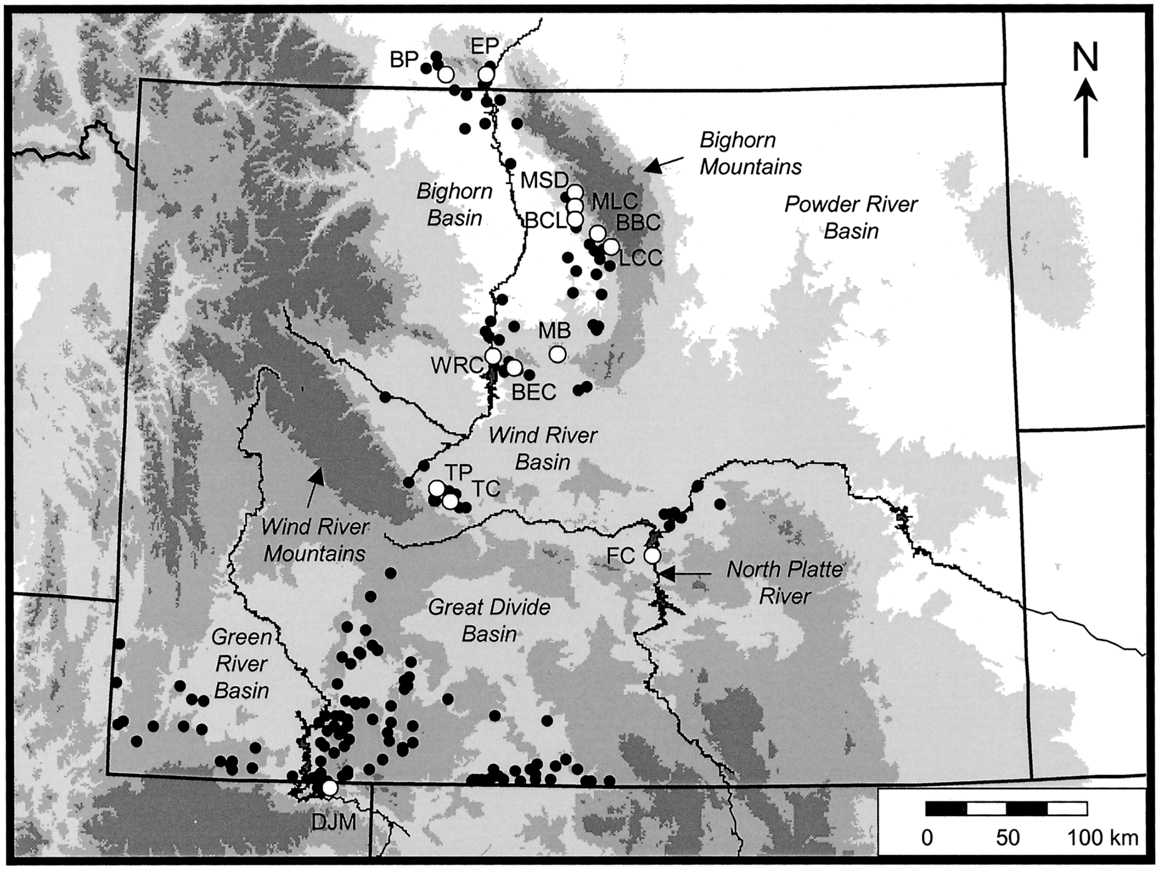

FIG. 2. Elevation map of Wyoming and adjacent Montana (white, 900–1550 m; light gray, 1500–2100 m; medium gray, 2100–2600 m; dark gray ≥2600 m). Black dots represent occurrences of Utah juniper documented from herbarium records (available online),[3] supplemented by field observations. Open circles represent midden-collecting sites. Initials for midden sites are as in Table 1.

lished data), and Utah juniper's northern limit was several hundred kilometers to the south (Fig. 1). Evidence is lacking for any refugial populations in these or adjacent regions. Early Holocene warming initiated migration of Utah juniper northward and eastward across the northern Great Basin and Colorado Plateau (Betancourt 1990, Thompson 1990, Nowak et al. 1994). Utah juniper reached the northeastern edge of the Colorado Plateau at the Utah/Colorado/Wyoming border by ~10.0 ka (Sharpe 1991, 2002).

The scattered populations of Utah juniper in the lowlands of north central Wyoming and adjacent Montana (Figs. 1 and 2) comprise ideal circumstances for studying effects of landscape structure and climate variability on natural invasion. These populations are concentrated in regions of exposed, slowly weathering bedrock, primarily along the flanks of mountain ranges, between 1100 and 2100 m elevation (Wight and Fisser 1968, Knight 1994) (Fig. 2). Populations are absent from alkaline and clay-rich soils, as well as from the extensive low basins (Green River, Continental Divide, Wind River, Bighorn, Powder River) that separate Wyoming's mountain ranges (Fig. 2). Thus, the species distribution is not only structured by landscape heterogeneity, it is also concentrated in areas where woodrat middens are most likely to be preserved for documentation of invasion patterns. The region has undergone substantial climatic variation during the Holocene, documented from independent records (Lyford et al. 2002).

We present results of analyses of 205 radiocarbon-dated woodrat middens from 14 sites in Wyoming and adjacent Montana and Utah, systematically sampled to provide the best possible record of spatiotemporal patterns of invasion of Utah juniper during the Holocene. We use a GIS-based approach to assess how landscape structure (i.e., spatial variation in climate, elevation, bedrock, and surficial materials) influences the modern distribution of Utah juniper in the region. Objectives of our study are to identify the spatiotemporal patterns of Holocene invasion of Utah juniper, and to assess the relative roles of landscape structure, long-distance dispersal, and environmental variability in determining those patterns.

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[3] URL: ⟨http://www.rmh.uwyo.edu⟩

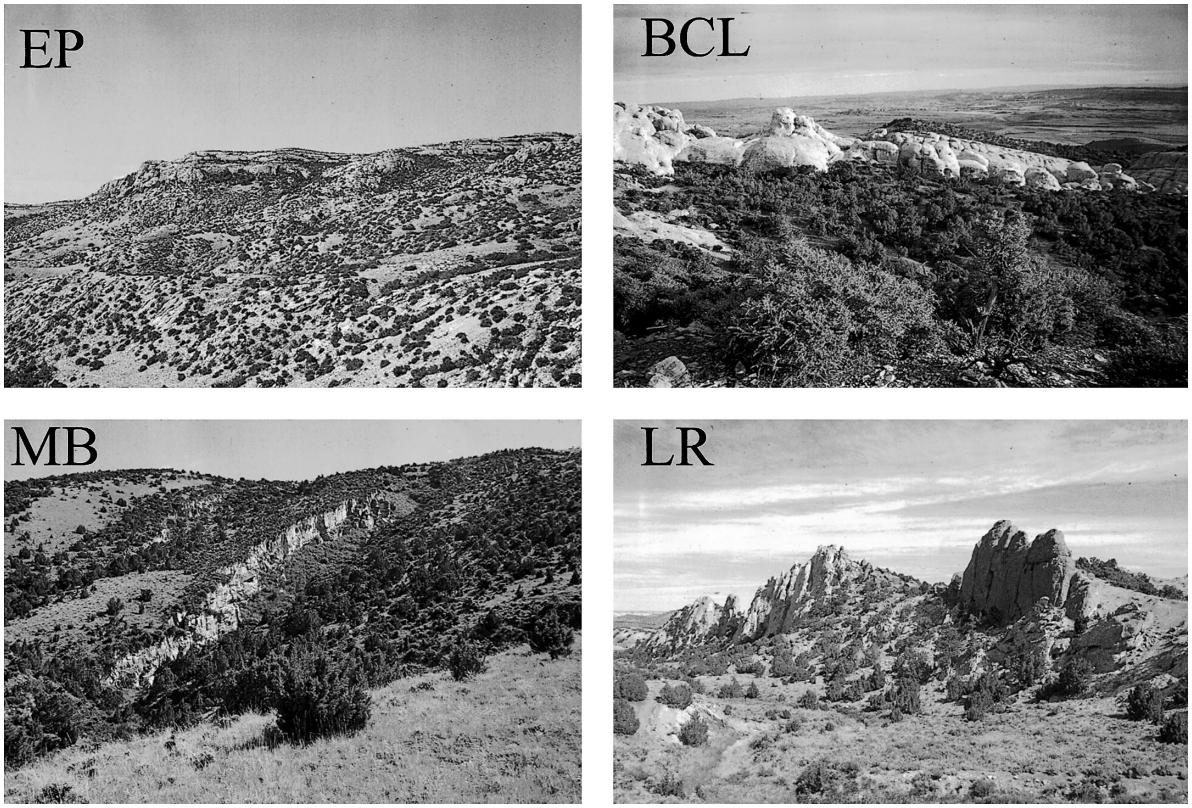

FIG. 3. Photographs of woodrat-midden sites within Utah juniper woodlands on limestone slopes in the eastern Pryor Mountains (EP) of southern Montana; sandstone ridges of Buffalo Creek Lookout (BCL), west-central Bighorn Mountains, Wyoming; limestone canyon at Mahogany Butte (MB) southwestern Bighorn Mountains; and sandstone outcrops of Lakota Ridge (LR), near Fremont Canyon on the North Platte River.

METHODS

Study area

The scattered populations of Utah juniper in Wyoming and Montana occur in woodlands on coarse-textured bedrock outcrops and colluvium on the flanks of major mountain ranges (Wind River Mountains, Bridger Mountains, Bighorn Mountains, Pryor Mountains) and on isolated escarpments and anticlines in structural basins (Fig. 2). The woodlands are concentrated in areas of sandstone and limestone bedrock, although they occur locally on granites and metamorphic rocks in Wind River Canyon and near Fremont Canyon, and also occur on coarse-textured tills of Bull Lake moraines on the southeastern flanks of the Wind River Range. All of these woodlands are between 1100 and 2100 m elevation.

Utah juniper is dominant in most of these woodlands, and is frequently the only large shrub species present (Fig. 3). *Juniperus scopulorum* is codominant with Utah juniper at higher elevations and on mesic sites (shaded canyons and canyon floors, bedrock seepage areas). *Cercocarpus ledifolius* is abundant in many Utah juniper woodlands in the Pryor Mountains and eastern Bighorn Basin (Wight and Fisser 1968, Knight et al. 1987). Pinyon pine (*Pinus edulis*) and Utah juniper are codominant at our southernmost site, Dutch John Mountain. This latter site is within 5 km of the northernmost population of pinyon pine, and is floristically and structurally similar to pinyon/juniper woodlands of the Colorado Plateau to the south. *Artemisia tridentata* occurs locally in most Utah juniper woodlands throughout the study region. Grasses and forbs occur as scattered individuals or populations between the shrubs in these woodlands. Woodlands dominated by Utah juniper are typically bordered by *Artemisia tridentata* steppe at lower elevations, and by montane forests (*Pinus flexilis*, *P. ponderosa*, *Pseudotsuga menziesii*, *J. scopulorum*, *Populus tremuloides*) at higher elevations.

Sampling strategy

We collected, radiocarbon-dated, and analyzed 205 middens formed by bushy-tailed woodrats (*Neotoma cinerea*) at 14 sites in central Wyoming, south-central Montana, and northeastern Utah (Fig. 2, Table 1). Utah juniper is dominant or codominant in woodlands at all of these sites (Fig. 3, Table 1). Midden series from these 14 sites comprise a spatial array for tracking the

TABLE 1. Site characteristics for study areas.

Latitude	Longitude	Elevation (m)	Bedrock†	Dominant aspect	Dominant species‡	No. middens	Age range (yr BP)§
East Pryor Mountain, Southern Bighorn Canyon (EP)							
45°02′	108°16′	1275–1590	Madison LS, Tensleep SS	all	*J. osteosperma*, *C. ledifolius*	37	510–30 110
Big Pryor Mountain (BP)							
45°08′	108°38′	1490–1565	Tensleep SS	S	*J. osteosperma* (*J. scopulorum*, *P. flexilis*)	22	520–11 315
Meyer Spring Draw (MSD)							
44°22′	107°33′	1840–1880	Tensleep SS	W	*J. osteosperma*	6	290–5425
Medicine Lodge Canyon (MLC)							
44°18′	107°31′	1510–1645	Tensleep SS	W	*J. osteosperma*	12	1315–8600
Buffalo Creek Lookout (BCL)							
44°09′	107°30′	1490–1505	Tensleep SS	W	*J. osteosperma*	10	0–3280
Brokenback Canyon (BBC)							
44°06′	107°25′	1505–1585	Tensleep SS	SE	*J. osteosperma*	8	115–3355
Lower Canyon Creek (LCC)							
44°02′	107°20′	1490–1600	Madison LS	S, SW	*J. osteosperma*	6	600–1820
Mahogany Butte (MB)							
43°38′	107°21′	1635–1660	Tensleep SS, Madison LS	W, E, NE, NW	*J. osteosperma*, *C. ledifolius*	13	0–8410
Wind River Canyon (WRC)							
43°33′	108°12′	1365–1425	Amsden LS, Phosphoria LS	W, SW	*J. osteosperma* (*J. scopulorum*)	13	465–3875
Birdseye Creek (BEC)							
43°23′	108°05′	1630–1675	Phosphoria LS	W, SW, SE, NE	*J. osteosperma*	3	45–3350
Tweaver Pass (TP)							
42°42′	108°33′	1850–1855	Nugget SS	SW	*J. osteosperma*	5	1025–4545
Fremont Canyon (FC)							
42°29′	106°47′	1665–1870	Tensleep SS, Madison LS	S, SE	*J. osteosperma* (*J. scopulorum*, *P. flexilis*, *P. ponderosa*)	14	165–8930
Twin Creek (TC)							
42°40′	108°30′	1815–1900	Nugget SS	all	*J. osteosperma*	9	0–1875
Dutch John Mountain (DJM)							
40°57′	109°00′	1980–2070	Navajo SS	S (SE, SW)	*J. osteosperma*, *P. edulis*	47	465–39 820

† LS refers to limestones (occasionally grading into dolomites). SS refers to sandstones.

‡ Dominant species in woodlands at the site. Species in parentheses include subdominants, usually consisting of scattered individual trees and shrubs.

§ Samples post-dating 24 000 ^{14}C yr BP were converted to calendar years BP using the Intcal 98 calibration curve, based on Method A (ranges with intercepts) from CALIB 4.3 (Stuiver and Reimer 1993, Stuiver et al. 1998). Samples predating 24 000 ^{14}C yr BP were converted using CalPal_A (available online).[4]

spatiotemporal patterns of Utah juniper invasion in the region. We note the singularity of this geographically extensive synoptic survey to track the migration of a single species. The midden collection was carried out mostly during two field seasons and involved field crews of 5–10 people. Woodrat-midden sampling has traditionally involved 1–2 people collecting 10–20 middens for a single chronology, limited in part by available funds for radiocarbon dates. More recently, larger field crews are being deployed to canvass larger outcrops and generate series of 50–100 middens from a single site or elevation, or in our case, multiple chronologies from many sites along a presumed pathway of invasion. Ready access to vacuum gas lines for pretreatment of plant macrofossils to gas–CO$_2$ and graphite targets and the associated discounts for age estimation using tandem accelerator mass spectrometry now make these synoptic approaches feasible.

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[4] URL: ⟨http://www.calpal.de⟩

Use of midden macrofossil data in our application requires three critical assumptions: (1) presence/absence of Utah juniper macrofossils in middens is a reliable means for inferring presence/absence of the species in surrounding vegetation (within ~100 m), (2) presence/absence of Utah juniper near a given midden site is a reliable means for inferring presence/absence in vegetation of the study area (canyon or escarpment) (within 1–5 km), and (3) the study areas from which woodrat middens were collected are representative of the region, or at least of the habitats suitable for colonization by Utah juniper populations.

The first assumption, that Utah juniper is reliably represented in woodrat-midden macrofossil assemblages, has been critically evaluated by Lyford et al. (2003). Their study of 59 modern middens from five sites in our study region (all similar in vegetation and topography to our study sites) indicates that individuals of *Neotoma cinerea* have a strong preference for juniper, particularly Utah juniper, in constructing middens. Utah juniper occurred in all middens where Utah juniper trees grew within 30 m, regardless of whether Utah juniper occurred as dense woodland or as a single, isolated individual in sagebrush steppe (Lyford et al., *in press*). Thus, presence/absence of Utah juniper macrofossils in middens are reliable for inferring presence/absence in local vegetation.

The second assumption, that presence/absence of Utah juniper from the vicinity of a midden site (i.e., within 100 m radius) is representative of a study area (a larger area within 1–5 km), is more difficult to evaluate directly. The question revolves around whether small, isolated populations of Utah juniper at a study site could go undetected in our sampling network because no individuals happened to grow near midden localities. We acknowledge this possibility, but note that when Utah juniper is present in a canyon or escarpment in our study region, it is nearly always dominant or codominant, with populations concentrated near the bedrock exposures where middens are preserved (Fig. 3). This situation may not always have prevailed; Utah juniper populations may have been small and isolated at some study sites under different climatic regimes of the past. However, at each of our study sites, the first occurrence of Utah juniper in the midden record is followed by continuous occurrence in all younger middens (see Appendix and *Results*). There are no reversals, suggesting that once Utah juniper populations were established at any study site, they quickly expanded to occupy available sites throughout the canyon or escarpment.

The final assumption, that our study sites are representative of the region as a whole, particularly with respect to the course of Utah juniper invasion, is reasonable in view of the fact that the densest and most extensive populations of the species are concentrated in areas where limestones and sandstones are extensively exposed (Knight 1994). Although Utah juniper is capable of growing on deeper, fine-textured soils, populations at such sites are generally young, having been formed only in the past century (Wight and Fisser 1968, Waugh 1986). Evidence of previous occupation of these sites by Utah juniper (e.g., stumps, dead wood) is lacking, even though dead juniper stumps and wood are abundant in adjacent bedrock areas (S. T. Jackson, S. T. Gray, J. L. Betancourt, and M. E. Lyford; *personal observations* and *unpublished data*).

Our bedrock-dominated study sites represent the habitats that Utah junipers would have colonized first, and are coincidentally well suited for preservation of fossil woodrat middens. Jackson et al. (1997) noted that fine-grained sensors (e.g., macrofossil assemblages) could be used synoptically to represent coarse-grained patterns (subcontinental species ranges and invasion patterns) provided that (1) the species of interest had a high likelihood of being represented in fossil assemblages given occurrence in local vegetation, and (2) the species had a high likelihood of occurring in vegetation near study sites if it occurred anywhere in the region (e.g., a species that produced abundant and preservable seeds or foliage and preferred wet habitats such as lakeshores). Our study design fits those criteria.

Woodrat-midden analysis

We conducted exhaustive searches for fossil woodrat middens at each of the 14 study sites, walking along cliff faces and bedrock exposures, checking cavities (caves, overhangs, crevices) for middens. The number and age range of middens varied among study sites (Table 1). In the field, middens were removed using a hammer and chisel, inspected, described, and cleaned before wrapping for transport. In the laboratory, middens were reinspected for integrity and possible contaminants, disaggregated in water, sieved (2-mm and 1-mm mesh), and dried. Presence or absence and relative abundance (1 = single occurrence to 5 = dominant; Spaulding et al. 1990) of Utah juniper and other macrofossils were determined for each midden by sorting the entire 2-mm sieve fraction and carefully inspecting the 1-mm fraction. For all middens where Utah juniper was either absent or abundant (relative abundance 3–5), we obtained ^{14}C dates from *Neotoma* fecal pellets using conventional beta counting. We routinely dated Utah juniper foliage and/or seeds directly by Accelerator Mass Spectrometry (AMS) in middens where they were in low abundance, or where we suspected temporally mixed assemblages (Lyford et al. 2002, Jackson et al. 2002).

Habitat suitability analysis

We developed an empirical model of habitat suitability for Utah juniper in Wyoming and southern Montana using a Weights of Evidence (WOE) geographic information system (GIS) approach. WOE has been applied extensively in minerals exploration[3] (Xu et al. 1992, Bonham-Carter et al. 1994) and has recently been adapted to biological applications including studies of rare bird habitat (Lenton et al. 2000) and distributions of fossil packrat middens (Mensing et al. 2000). In a manner similar to multiple regression techniques, the WOE approach involves the estimation of a response variable (probability of occurrence for the item under study in a given location) from a set of predictor variables. More specifically, the WOE approach compares a set of training points (known locations for the item under study) against a set of evidential themes (GIS-based maps showing different classes of variables thought to influence the distribution of the item under study)[5] (Bonham-Carter et al. 1988, Bonham-Carter 1994). Weights (favorability ratings) are then assigned to the classes within each evidential theme based on the spatial correlation between the class and the training data set. Both positive and negative occurrences are considered, and weights are calculated relative to the total area occupied by a class within the study region. The weights from all evidential theme maps are then summed to produce a probability-of-occurrence map showing areas of varying suitability for the presence of the item under study.

Our training data set consisted of 141 Utah juniper occurrences documented at the University of Wyoming Rocky Mountain Herbarium,[6] which has completed extensive floristic surveys throughout the region (Fig. 2). These occurrences were compared with evidential themes describing climate and substrate. We used output from the PRISM model[7] (Daly et al. 1994) to estimate monthly and annual temperature and precipitation for our study region as well as an index of moisture stress (defined as the ratio of growing-season precipitation to growing-season temperature) as our climatic themes. The latter index has proven useful in modeling tree performance in western North America (Rehfeldt et al. 1999), and improved model performance over using temperature and precipitation estimates alone. We tested various combinations of two to 12 climate variables, including monthly and seasonalized mean temperature and precipitation, for their ability to describe the current distribution of Utah juniper. After the initial testing, we selected three evidential themes for the climate analyses: total annual precipitation, mean annual temperature, and the ratio of summer (June, July, and August) precipitation to summer temperature. For substrate themes, we used maps of soil (USDA 1994), bedrock, and surficial-material types.[8,9] Bedrock formations were aggregated by lithologic type to condense more than 100 classes into 13 groups and to facilitate correlations between Wyoming and Montana geological maps. Maps of soils and surficial types were similarly condensed to 40 and 27 categories, respectively. Our study region included all of Wyoming and adjacent portions of Montana up to 100 km north of the Wyoming border.

In order to explore the relative influence of climate and substrate on Utah juniper distribution, we conducted a series of WOE analyses using climate and substrate separately and then simultaneously. To assess the accuracy of the habitat analyses, we compared areas selected as the most suitable locations for Utah juniper occurrence (top 40% of locations by probability-of-occurrence) against mapped distributions of Utah juniper in Wyoming and Montana (Knight et al. 1987; Driese et al. 1997). All WOE analyses were conducted using the ArcWofE extension for the ArcView GIS program (ESRI, Redlands, California; see footnote 5) employing 4-km^2 grid cells based on the minimum resolution of the evidential themes.

RESULTS

Utah juniper habitat distribution

Our WOE analyses indicate that climate suitable for Utah juniper is widespread, covering over 37% of the study area (Fig. 4a). In contrast, Utah juniper populations cover only 7.6% of the area. Suitable climates are concentrated in the basins and foothills of western Wyoming. If climate were the only limiting factor, Utah juniper could potentially occupy nearly all of the basins of western and central Wyoming (Green River, Continental Divide, Wind River, Bighorn) as well as other low areas (Fig. 4). Utah juniper is not limited by high temperatures or low precipitation in Wyoming and Montana; its potential habitat includes the hottest and driest parts of the region (Martner 1986; National Climatic Data Centers CLIMAPS database [available online][10]). The species is limited by cool temperatures and high precipitation, however; high elevations ($>$2200 m) in the mountains of central and western Wyoming are unsuitable (Fig. 4a). Climate associated with high suitability for Utah juniper consisted of high annual temperatures (3.8–6.7°C) and hot summers (16.1–21.6°C), with annual precipitation ranging from 22 to 50 cm.

Substrates suitable for Utah juniper are much more restricted than climate, comprising 3.2% of the study area (Fig. 4b). More than 91% of the area classified as highly suitable substrate is within the current distribution of Utah juniper (Fig. 4d). Suitable substrates consisted of coarse-textured soils, particularly in regions of resistant sandstones and coarse shales (often interbedded with sandstones). Highly suitable surficial materials consisted primarily of rock outcrops, but also included colluvial deposits. Combining the substrate and climate evidential themes yielded a small increase in the number of sites classified as highly suitable (Fig. 4c).

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[5] URL: ⟨http://ntserv.gis.nrcan.gc.ca/wofe/index.html⟩

[6] URL: ⟨http://www.rmh.uwyo.edu⟩

[7] URL: ⟨http://www.ocs.orst.edu/prism⟩

[8] URL: ⟨http://www.sdvc.uwyo.edu⟩

[9] URL: ⟨http://nris.state.mt.us/gis/gis.html⟩

[10] URL: ⟨http://www.nndc.noaa.gov/cgi-bin/climaps/climaps.pl⟩

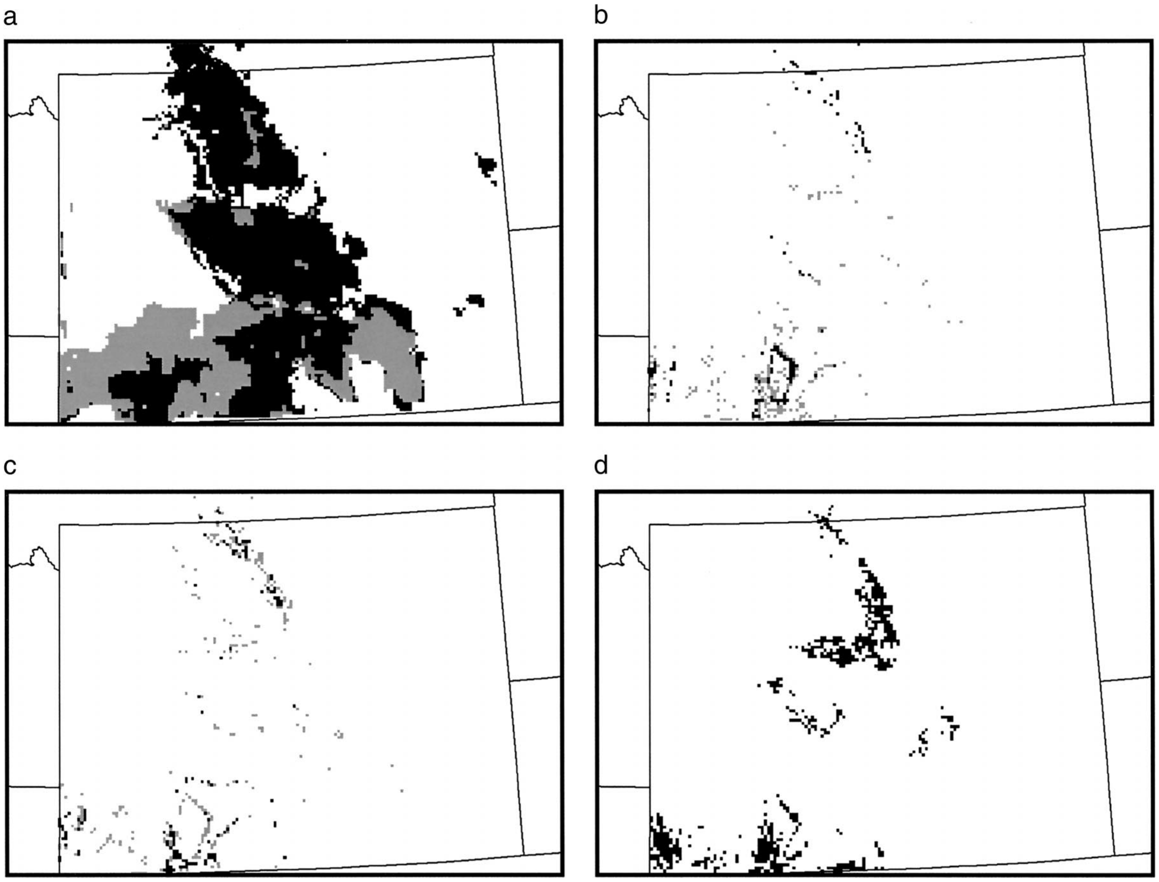

FIG. 4. Suitable habitats for Utah juniper in Wyoming and adjacent Montana. Areas shown in black indicate extremely suitable habitats, while gray areas indicate moderately to highly suitable habitats. (a) Climate (ratio of growing-season precipitation to growing-season temperature. (b) Substrate (including soil, bedrock, and surficial-material type. (c) Climate and substrate combined. (d) Modern distribution of Utah juniper (Knight et al. 1987, Driese et al. 1997; available online [see footnote 3]). Note that climate (a) overpredicts the distribution (d), which is strongly constrained by substrate variables (b), and that favorable habitat is patchily distributed (c).

Suitable habitats for Utah juniper are arrayed on the landscape as linear clusters (Fig. 4b–d), reflecting the linear alignments of exposed, uplifted sedimentary bedrock along the flanks of mountain ranges and other uplift features. These clusters are separated by extensive areas of unsuitable habitat, primarily fine-textured and alkaline substrates in the basins and all substrates in high-elevation mountain ranges and plateaus.

Utah juniper migration

Utah juniper macrofossils occur in the youngest middens at each of our 14 study sites, and are represented in successively older middens at each site until a point is reached at which they no longer occur (Fig. 5b; Appendix). There are no temporal reversals at any of our study sites, indicating that once Utah juniper populations colonized each site, they spread and persisted until the present. This pattern supports our assumption (see *Methods: Sampling strategy*) that individual midden samples are representative of their respective study sites, despite the fine-scale sampling of vegetation by individual middens.

The earliest occurrences of Utah juniper in our study region were at Dutch John Mountain in northeastern Utah, at 9.4 ka (Fig. 5c). This site has 11 middens predating the Holocene (not shown in Fig. 5). These middens range in age from 37.9 to 10.6 ka, and all lack macrofossils of Utah juniper, as do pre-Holocene middens from our other study sites (see Appendix). The absence of Utah juniper from pre-Holocene middens at our sites is consistent with previously published results from sites to the south (Fig. 1), and confirms that Utah juniper is a recent addition to the regional flora.

We lack data for southwestern Wyoming, where Utah juniper populations are widespread (Fig. 2) and where suitable habitats are extensive (Fig. 4). The continuity of populations and suitable habitat between Dutch John Mountain and the uplands separating the Green River and Continental Divide Basins, together with the rapid spread of Utah juniper across eastern Utah in the late-glacial (Betancourt 1990, Sharpe 1991), suggests that Utah juniper colonized southwestern Wyoming during the early Holocene (∼9.5–8.0 ka). However, additional midden studies are needed to evaluate this.

Utah juniper populations were established during the mid-Holocene (by 5.4 ka) at two sites (Mahogany Butte and East Pryor Mountain) in the Bighorn Basin region (Fig. 5d). Utah juniper colonization at these sites appears to have preceded establishment at sites to the south in the Bighorn and Wind River Basins (Fig. 5d, e). East Pryor Mountain currently hosts the northernmost populations of Utah juniper (Figs. 1, 2).

The primary portal for migration from southwestern Wyoming into north central Wyoming was most likely the southeastern Wind River Range (Fig. 2). Unfortunately, midden records from our sites in this region, Tweaver Pass and Twin Creek, span only the past 4.5 and 1.9 ka, respectively. Utah juniper occurs in all the middens at the latter site, and in all except the oldest one (4.5 ka) at Tweaver Pass (Fig. 5b). The oldest occurrence of Utah juniper at Tweaver Pass is 3.8 ka (Fig. 5b, e), which may serve as a minimum age of establishment for the region. However, midden records from the Bighorn Basin region to the north indicate that Utah juniper populations were established at some sites well before this time (as early as 5.4 ka). Utah juniper may have occurred in the southeastern Wind River Range before 3.8 ka, and gone undetected in our sensing network owing to the lack of older middens. Alternatively, the relatively high elevation of Tweaver Pass and Twin Creek may have constrained colonization by Utah juniper; initial populations in the southeastern Wind River Range may have been at lower elevations (e.g., Red Canyon [1750 m], where middens were poorly preserved). Utah juniper colonized the Fremont Canyon area along the North Platte River between 4.3 and 3.6 ka, the same time interval as for Tweaver Pass (Fig. 5e).

Mid-Holocene establishment of Utah juniper at Mahogany Butte and East Pryor Mountain (Fig. 5c) was followed by a 2600-yr delay in further colonization of sites in the Bighorn Basin (Fig. 5b, e–g). Sites less than 30 km from these two sites were not invaded by Utah juniper during this period. Populations at all of our study sites along the flanks of the Bighorn Basin and the northern edge of the Wind River Basin were established between 2.8 and 1.0 ka (Fig. 4f, g). The invasion appears to have stalled after 1.5–1.0 ka. For example, suitable habitat north of Meyer Spring Draw (Fig. 4) lacks Utah juniper populations (Fig. 2). Exposures of Tensleep Sandstone at Meyer Spring Draw and Upper Alkali Creek canyon between 1585 and 1890 m elevation are vegetated by dense Utah juniper woodlands. Outcrops of Tensleep Sandstone of similar aspect and elevation in Webber Canyon, 3.5 km to the north, support Rocky Mountain juniper woodlands, although a few Utah juniper seedlings have become established there within the past few decades (S. T. Jackson, *personal observation*). Utah juniper is absent from extensive outcrops of Tensleep Sandstone and various limestones at Trapper Canyon, 9 km north of Meyer Spring Draw.

DISCUSSION

Spatiotemporal patterns in natural invasions

Subcontinental-scale maps of isopolls, pollen-inferred arrival times, and plant macrofossil presence/absence from eastern North America and Europe show clear patterns of Holocene plant invasions in response to climatic change (Davis 1981, Huntley and Birks 1983, Webb 1987, 1988, Jackson et al. 1997). These maps often convey the impression that these invasions proceeded in a steady, wavelike fashion, with species colonizing new territory along advancing fronts. It has long been suspected that these maps mask spatial and temporal heterogeneities in invasion patterns (e.g., King and Herstrom 1997, Clark et al. 1998). Widespread pollen dispersal together with spatial interpolation imposes spatial smoothing on isopoll and other pollen-based maps. Temporal imprecision at individual sites together with temporal smoothing among sites may further mask spatial and temporal heterogeneity in invasion patterns. King and Herstrom (1997), using spatial analysis of pollen-inferred arrival dates at individual sites, have demonstrated spatial and temporal variations in migration rates for *Picea* and *Fagus* in eastern North America. Studies of pollen and, more recently macrofossils, in the western Great Lakes region, where site densities are unusually high, indicate that invasion patterns of *Tsuga canadensis*, *Fagus grandifolia*, and *Betula allegheniensis* were neither front-like nor constant in rate during the late Holocene (Davis 1987, Woods and Davis 1989, Davis et al. 1986, 1998, Parshall 2002, Jackson and Booth 2002). These spatial and temporal heterogeneities in invasion patterns are not well understood, but can be attributed to effects of long-distance dispersal events, landscape structure, and climate variability (Clark et al. 1998). ‘‘Cryptic refugia’’ (Stewart and Lister 2001) may also contribute to such heterogeneity (Ronce 2001), although care must be taken to discriminate between true refugia (i.e., persistence of local populations since the last glacial maximum) and isolated populations established by long-distance dispersal long before regional expansion.

The invasion of Utah juniper into Wyoming and Montana was characterized by discontinuous patterns in both space and time (e.g., Fig. 5). We use these patterns, together with our habitat analysis and independent paleoclimate records, to demonstrate that long-distance dispersal, landscape structure, and climate variability all played important roles in governing the spatial and temporal patterns of the invasion.

Long-distance dispersal events

Our data show clearly that multiple long-distance dispersal events played critical roles in the Holocene

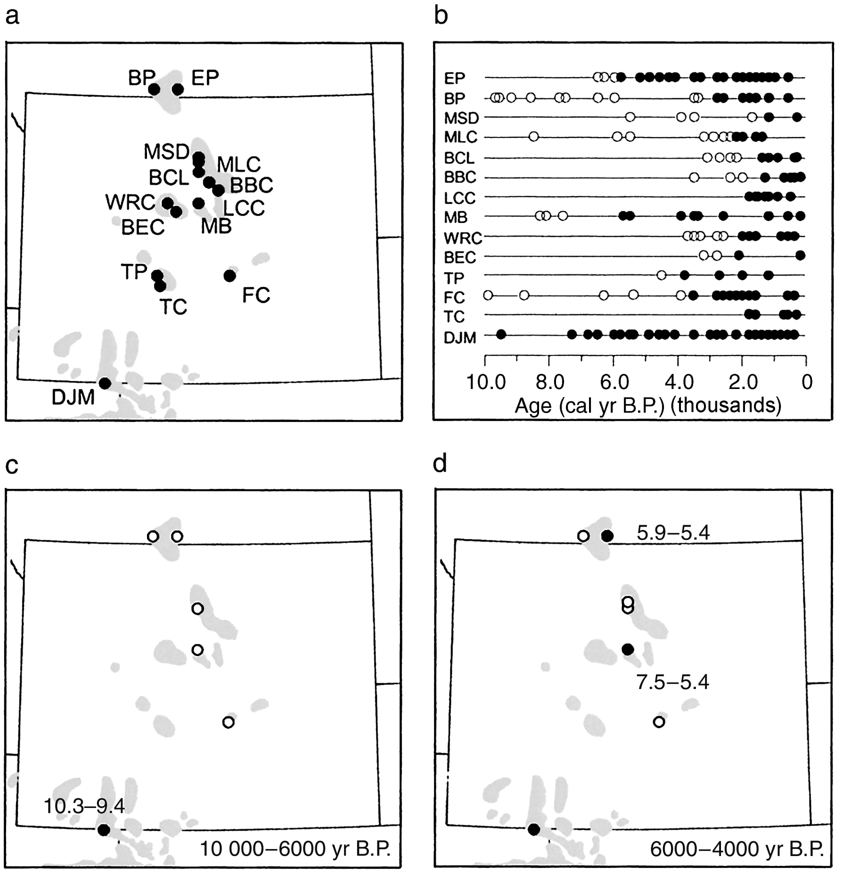

FIG. 5. Woodrat-midden records of Utah juniper invasion in Wyoming and adjacent regions. (a) Locations of woodrat-midden study sites (black circles) and modern distribution of Utah juniper (gray circles) in Wyoming and adjacent states. Modern distribution is from Little (1971). Site abbreviations are as in Table 1. (b) Holocene records of presence (filled circles) and absence (open circles) of Utah juniper macrofossils from woodrat middens at each of 14 sites (abbreviations are as in Table 1). Each symbol represents a single woodrat midden. Only middens postdating 10.0 ka are shown. Older middens at EP, BP, and DJM lack Utah juniper macrofossils (see Appendix). (c) Map of presence (filled circles) and absence (open circles) of Utah juniper macrofossils in woodrat middens dating between 10 and 6 ka. Only sites with at least one woodrat midden within this time interval are mapped. Numbers associated with Utah juniper occurrences denote dates (in thousands of years BP) of the youngest midden at the site that lacked Utah juniper macrofossils (e.g., 10.3 ka at DJM) and the oldest midden that contained Utah juniper macrofossils (9.4 ka). These dates bracket the date of Utah juniper colonization at the site. (d) Presence and absence of Utah juniper macrofossils between 6 and 4 ka. Sites with Utah juniper occurrences that lack associated numbers were colonized earlier (e.g., DJM). (e) Presence and absence of Utah juniper between 4 and 3 ka. (f) Presence and absence of Utah juniper between 3 and 2 ka. (g) Presence and absence of Utah juniper between 2 and 1 ka. (h) Number of study sites occupied by Utah juniper as a function of time in the mid-to-late Holocene. Only 11 of our 14 sites are plotted; LCC and TP were deleted because of absence or paucity of middens predating Utah juniper colonization, and DJM was not plotted because populations were established in the early Holocene.

invasion of Utah juniper in Wyoming and Montana. Colonization of suitable habitats on the flanks of the Bighorn and Wind River Basins required long-distance propagule dispersal events across unfavorable terrain in the Green River, Great Divide, and Wind River Basins, and over a low pass (2200–2400 m) at the southeastern end of the Wind River Range (Figs. 2, 4, 5). Dispersal distances ranged from 50 km (e.g., establishment in Wind River Range foothills) to 135 km (establishment of Fremont Canyon populations). If the Mahogany Butte and East Pryor Mountain populations originated from southwestern Wyoming (i.e., they preceded establishment of populations in the southeast Wind River Range and Wind River Canyon, as appears from our data [Fig. 5]), dispersal events of 240 to 370 km are implied.

Potential dispersal vectors for Utah juniper are obscure. Utah juniper seeds are dispersed primarily by lagomorphs and seed-caching rodents, in contrast to other juniper species, which are dispersed by birds, coyotes, and foxes (Schupp et al. 1996, 1997, Chambers et al. 1999). Dispersal from the Wind River Range foothills to Fremont Canyon may have been facilitated by human, animal, or water dispersal down the Sweetwater River Valley, which originates in the southeast Wind River Range and drains into the North Platte near

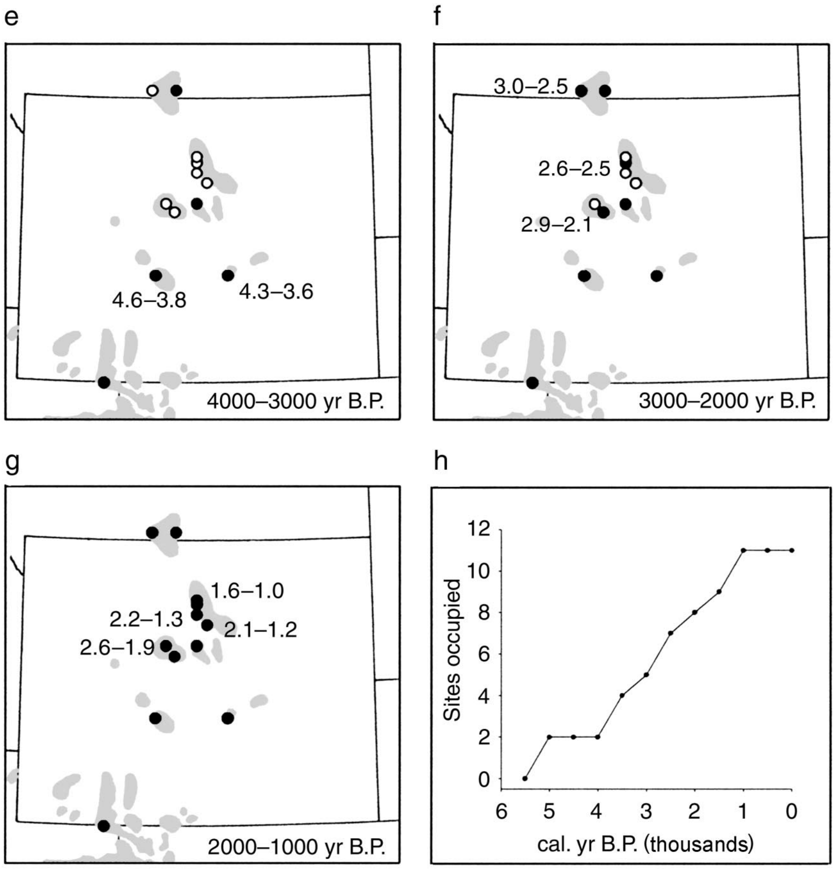

FIG. 5. Continued.

Fremont Canyon. Similarly, dispersal into the Bighorn Basin region may have proceeded along the Wind River/Bighorn River corridor, which runs from the southeast Wind River Range north through Wind River Canyon into the Bighorn Basin and, eventually, Bighorn Canyon (Fig. 2).

Regardless of the vector, it is clear that long-distance dispersal events occurred multiple times in the course of Utah juniper's migration in Wyoming and Montana. At millennial to multimillennial time scales, dispersal on the order of 100 km does not appear to have limited Utah juniper migration in the study region. The 2600-yr delay between establishment of initial populations (Mahogany Butte, East Pryor Mountain) and colonization of other sites in the Bighorn Basin (some as close as 30 km) is not likely to have arisen from dispersal limitations.

The role of long-distance dispersal events in natural invasions has been extensively discussed (Webb 1987, Clark 1998, Clark et al. 1998, 2001, Higgins and Richardson 1999, Ronce 2001). However, clear documentation of such events is often elusive because such events are rare and local, and observational networks (whether ecological or paleoecological) are usually of low spatial density and (in the case of pollen from lake sediments) coarse spatial resolution. Our study, by using a fine-scale sensor of Utah juniper presence/absence (macrofossils in middens) from an array of study sites concentrated in habitats that were particularly suitable for Utah juniper, shows clearly that dispersal events spanning 10–100 km occurred multiple times during the Holocene.

Our data do not indicate the precise seed source of each colonization event, nor do they indicate whether existing populations at a site derived from more than one dispersal/colonization event. However, they provide a basis for a series of hypotheses on the spatial patterns and temporal sequence of the invasion. For example, we hypothesize that all of the extant populations in the North Platte valley (Fremont Canyon and vicinity) derived from one or a few colonization events, that the source population was in the southeastern Wind River Mountains, and that the North Platte populations did not contribute to colonization of sites to the north in the Wind River and Bighorn Basins (Figs. 2, 5). We also hypothesize that the mid-Holocene populations established at Mahogany Butte and East Pryor Mountain served as critical (perhaps sole) propagule sources for the late Holocene expansion in the Bighorn Basin region. Studies of genetic diversity and genetic markers in Utah juniper populations throughout the region may provide tests of these and similar hypotheses.

Landscape structure

The invasion of Utah juniper into Wyoming and Montana was constrained by the spatial distribution of suitable habitat, the latter consisting of midelevation exposures of sandstones and other suitable lithologies. These habitats are neither uniformly nor randomly distributed on the Wyoming landscape; they are concentrated along the flanks of the mountain ranges that rim structural basins, and on local escarpments within the basins. These suitable habitats represent the targets for long-distance-dispersal events that lead to successful establishment of populations. In the absence of knowledge of the dispersal vector involved, we cannot assess whether the spatial distribution enhanced, inhibited, or did not affect such dispersal. In the absence of Utah juniper, these same habitats are occupied by woodlands dominated by Rocky Mountain juniper (Jackson et al. 2002, Lyford et al. 2002). Those woodlands might have comprised attractive dispersal targets for avian dispersers.

Suitable habitats for Utah juniper in Wyoming comprise a series of widely dispersed, large linear features (Fig. 4). Suitable sites are either well connected within each of the linear clusters (e.g., the corridor of suitable habitat along the west flank of the Bighorn Range) or are separated by only a few kilometers (e.g., suitable habitats within the Fremont Canyon area and the southeastern Wind River Range) (Fig. 4c). The clusters themselves are widely dispersed (30–130 km apart). This pattern suggests that the most critical steps in Utah juniper invasion were the long-distance dispersal events among clusters; presumably, once a population was established in a given region, dispersal events on the order of 1–10 km would ensure rapid spread and infilling within that region. Thus, lack of suitable habitat, at least in terms of appropriate bedrock and surficial materials, cannot account for the 2600-yr delay between initial establishment in the Bighorn Basin (Mahogany Butte and East Pryor Mountain) and subsequent spread to other sites in the region (Fig. 5d–g).

Climate variability

The invasion of Utah juniper in Wyoming and Montana was episodic (Fig. 5). Major establishment events are recorded between 7.5 and 5.4 ka (Mahogany Butte and Southern Bighorn Canyon), 4.6 and 3.6 ka (Tweaver Pass and Fremont Canyon), and 3.0 and 1.0 ka (various sites in the Bighorn Basin region). No new colonizations were recorded in the Bighorn Basin region between 5.4 and ~3.0 ka.

The alternating expansions and stillstands of Utah juniper in the Bighorn Basin correspond clearly to independently recorded climatic variations in the region, with expansion occurring during periods of relative drought and warmth and pauses occurring during moist, cool intervals. The first period of expansion (~7.5 to 5.4 ka) occurred during a warm, dry period recorded both locally and regionally. The elevation of lower treeline (limber pine) at East Pryor Mountain, which is inversely correlated with available moisture, was relatively high between at least 6.4 ka and 5.0 ka (Lyford et al. 2002). At Big Pryor Mountain, *Atriplex* macrofossils (indicating warm and dry conditions) were abundant in middens between 9.2 and at least 6.3 ka, and Chenopodiaceae pollen was particularly abundant during this period (Lyford et al. 2002). Relatively warm and/or dry conditions before 5.0 ka are also evident in pollen records from the central Rockies (Whitlock 1993, Whitlock and Bartlein 1993, Fall et al. 1995), and lake-level (Fritz et al. 1991, Valero-Garces et al. 1997) and geomorphic records (Muhs 1985, Forman et al. 1995, 2001, Madole 1995, Fredlund and Tieszen 1997) from the northern Great Plains.

The cessation of Utah juniper expansion in the Bighorn Basin and northern Wind River Basin after 5.4 ka corresponds to a transition to relatively wet climatic conditions. Lower treeline at East Pryor Mountain descended nearly 500 m, and *Atriplex* disappeared from middens at Big Pryor Mountain (Lyford et al. 2002). A cool, relatively moist, period between 5.4 and 2.8 ka is recorded at many sites in the central Rockies and adjacent Great Plains by dune stabilization (Dean et al. 1996), reduction in crownfire-induced alluvial deposition (Meyer et al. 1995), transition to mesic forests (Mehringer et al. 1977, Barnosky 1989, Whitlock 1993), lake-level rises (Valero-Garcés et al. 1997), and lowering of both upper (Fall et al. 1995) and lower treeline (Lyford et al. 2002).

The main expansion of Utah juniper in the Bighorn Basin, which involved backfilling of sites bypassed during the initial long-distance dispersal events, occurred when climate became warmer and drier again, between 2.8 and 1.0 ka (Fig. 4). Lower treeline retreated upward 500 m at East Pryor Mountain after 2.8 ka (Lyford et al. 2002). This climatic change is widely recorded at other sites in the central Rockies and Northern Plains.

Population establishment at Tweaver Pass (between 4.6 and 3.8 ka) and Fremont Canyon (between 4.3 and 3.6 ka) occurred during the cool, moist period when invasion was interrupted in the Bighorn Basin and northern Wind River Basin (Fig. 5e). They may have been established during one or more transient dry periods. Although we have found no clear evidence of dry intervals in the region between 5.4 and 2.8 ka, we note that most paleoclimatic records in the region lack sufficient sensitivity and temporal precision to detect centennial-scale events.

Interaction of climate variability with dispersal and landscape structure

Natural and exotic plant invasions require dispersal of propagules to suitable sites under favorable conditions. The rain of propagules on unoccupied sites will depend on distance of those sites from source populations, dispersal mechanisms, and population size at the source (i.e., seed source strength). Sites suitable for colonization form mosaics on the landscape, which will vary among species depending on their recruitment niche and among regions depending on the texture of the underlying environmental variables. This texture may range from extremely fine-grained (e.g., very small sites that are closely spaced and widely distributed) to extremely coarse-grained (very large patches of suitable habitat that are widely separated). Climate variability at interannual, decadal, centennial, and millennial time scales can lead to periods of rapid expansion (e.g., by increasing the density and connectedness of sites suitable for recruitment) alternating with periods of quiescence (e.g., most unoccupied sites are rendered unsuitable for recruitment). Climate variability, by controlling population size and resource allocation at previously colonized sites, also influences seed source strength and hence the propagule rain at unoccupied sites.

All of these factors played important roles in the invasion of Utah juniper. Dispersal and landscape structure have been much discussed in the literature, although effects of landscape structure on past and future invasions is in particular need of further exploration (Ronce 2001, With 2002). Climate variability has been neglected in treatments of natural and exotic invasions, even though climate varies at all time scales relevant to invasions (Swetnam and Betancourt 1998, Swetnam et al. 1999, Jackson and Overpeck 2000). We note that effective moisture in the central Rockies varies at significant multidecadal periodicities, particularly in the >40 yr domain, and that the frequency and strength of these multidecadal signals varies through time (Gray et al. 2003). Such nonstationary multidecadal oscillations may play a critical role in modulating the probabilities of successful colonization and the pace and timing of expansion.

Furthermore, climate variability influences both dispersal and landscape structure. Propagule source strength is a function of both population size and individual fecundity at source sites, and both of these factors will vary according to climate. Propagule source strength will increase during climatic intervals favorable to recruitment and productivity of source populations. In general, frequency of long- and short-distance dispersal events should increase during favorable climate intervals, although climate may interact with dispersal mechanisms and/or vectors.

The lack of colonization in the Bighorn Basin during the wet period 5.4–2.8 ka may have resulted from low source strength at the populations that were established earlier. If these populations remained small and/or unproductive during this period, dispersal to other suitable sites would have been dampened. Any favorable climatic intervals that might have occurred during that period may have been of insufficient duration to provide an increase in propagule source strength sufficient to colonize other sites. Although this hypothesis begs the question of why the Tweaver Pass and Fremont Canyon populations were successfully established during that period, it may be relevant that source populations were extensive in southwest Wyoming, closer to those sites (Fig. 2).

Climate variability also influences the mosaic of suitable sites for an invading species. Density, areal extent, and connectedness of suitable sites may vary dramatically with temporal variations in climate. Targets for dispersal from existing populations may alternate between large and extensive during certain climate regimes and small and dispersed during others. The 220-m elevational difference between the Bighorn Basin sites first colonized by Utah juniper (Mahogany Butte and East Pryor Mountain) suggests that a broad expanse of potential dispersal targets existed in the region during the period of favorable climate before 5.4 ka, increasing the likelihood that rare, long-dispersed seeds would land on suitable habitat.

Woody plants are particularly capable of thriving or at least surviving as adults in a variety of circumstances; the regeneration niche is typically narrower than the niche for adult survival and reproduction (Grubb 1977). This may explain why Utah juniper populations were able to persist at Mahogany Butte and East Pryor Mountain for more than 2000 years while no new sites in the Bighorn Basin were invaded. The ability of woody plants to establish populations during transient periods of favorable climate and persist during unfavorable periods may be critical in their ability to invade new territory. Small advance populations can serve as seed sources when climatic conditions become favorable, accelerating colonization of new territory (Moody and Mack 1988). For example, if Utah juniper had not established a few isolated populations in the Bighorn Basin during the mid-Holocene, it might be far less extensive and abundant in the region today.

Demographic studies (Wight and Fisser 1968, Waugh 1986) and repeat photography (see the University of Arizona Desert Laboratory web site)[11] at many of our sites in central and northern Wyoming show rapid increase in Utah juniper tree densities during the last 100 years. The Late Holocene establishment of Utah juniper in much of this region suggests that these expansions may represent continued population growth and infilling associated with initial invasion. However, Utah juniper density is increasing at sites spanning a broad range of initial establishment dates (5.4–1.0 ka). Upslope expansion of Utah juniper and Rocky Mountain juniper at Meyers Spring Draw, the most recently colonized site, has been initiated within the past century (S. T. Jackson and S. T. Gray, *unpublished data*). Grazing, fire reduction, and/or 20th century climate change

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[11] URL: ⟨http://wwwpaztcn.wr.usgs.gov/wyoming/⟩

are probably responsible for the recent Utah juniper expansions, as has been documented for other native woody species elsewhere in western North America (Swetnam et al. 1999).

Conclusions

Our study demonstrates the key roles of long-distance dispersal, landscape structure, and climatic variability in governing the pattern and pace of natural invasion in response to climatic change. Long-distance dispersal has been a major focus of invasion research and modeling (Shigesada and Kawasaki 1997, 2002, Clark 1998, Clark et al. 2001, Nathan et al. 2002). Landscape structure and temporal environmental variability have also been recognized and discussed by ecologists (Johnstone 1986, Higgins and Richardson 1996, With 2002). Both deserve closer attention, particularly in efforts at modeling and predicting the course of invasions. Invasion models that treat environmental variation as stationary stochastic patterns in space and time, and that emphasize internal mechanisms of population processes in determining rates of spread (e.g., Mack 1995, Williamson 1996, Shigesada and Kawasaki 1997) may be insufficient. Environmental heterogeneity consists of broadscale geographic gradients upon which are superimposed nonstationary mosaics of edaphic and topographic variation across a range of spatial scales. Initial colonizations may be concentrated at particularly favorable sites far distant from the source populations (Jacobson 1979, Betancourt et al. 1991).

Past and future migrations may follow neither a front-like advance nor a random pattern of long-distance colonizations, but rather a process of long-distance colonization, expansion, and backfilling that is partly predictable from the environmental mosaic. Migration rates may be governed more by climate variability at time scales ranging from interannual and decadal to millennial than by internal population dynamics. Observed accelerations and decelerations of invasive spread (Williamson 1996, Shigesada and Kawasaki 1997) may represent alternating climatic regimes particularly favorable and unfavorable for colonization, respectively. Successful prediction of natural invasions may hinge on understanding how the various modes of climate variability shift the environmental mosaic, and thus modulate the probabilities of long-distance colonization, persistence, and expansion of founder populations. The observations that most introductions of non-native species appear to fail multiple times before they eventually succeed, and that population expansion is often long-delayed after initial colonization (Sax and Brown 2000), may be attributable to landscape heterogeneity and climatic variability and their interactions.

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APPENDIX

An inventory of all woodrat middens analyzed in this study, including site location, midden sample number, radiocarbon and calendar-year age, dated material, and presence or absence of macrofossils of Utah juniper is available in ESA's Electronic Data Archive: *Ecological Archives* M073-006-A1.