ROLE OF MULTIDECADAL CLIMATE VARIABILITY IN A RANGE EXTENSION OF PINYON PINE

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Abstract. Evidence from woodrat middens and tree rings at Dutch John Mountain (DJM) in northeastern Utah reveal spatiotemporal patterns of pinyon pine (*Pinus edulis* Engelm.) colonization and expansion in the past millennium. The DJM population, a northern outpost of pinyon, was established by long-distance dispersal (~40 km). Growth of this isolate was markedly episodic and tracked multidecadal variability in precipitation. Initial colonization occurred by AD 1246, but expansion was forestalled by catastrophic drought (1250–1288), which we speculate produced extensive mortality of Utah Juniper (*Juniperus osteosperma* (Torr.) Little), the dominant tree at DJM for the previous ~8700 years. Pinyon then quickly replaced juniper across DJM during a few wet decades (1330–1339 and 1368–1377). Such alternating decadal-scale droughts and pluvial events play a key role in structuring plant communities at the landscape to regional level. These decadal-length precipitation anomalies tend to be regionally coherent and can synchronize physical and biological processes across large areas. Vegetation forecast models must incorporate these temporal and geographic aspects of climate variability to accurately predict the effects of future climate change.

Key words: drought; founder event; paleoecology; pinyon–juniper woodlands; tree rings; vegetation change; woodrat middens.

INTRODUCTION

As a result of continuing drought and related disturbances, ecosystems throughout western North America are undergoing significant structural and demographic change, the likes of which have not been seen since the epic droughts of the 1930s and 1950s (Allen and Breshears 1998, Peters et al. 2004, Breshears et al. 2005). Precipitation-sensitive tree-ring records show that severe and extensive droughts spanning years to decades, often followed by prolonged wet periods, have been a common feature of western North American climate over the past 1000 yr (Swetnam and Betancourt 1998, Gray et al. 2003, Cook et al. 2004). Such dry–wet oscillations can reset demographic clocks (Swetnam and Betancourt 1998, Betancourt et al. 1993), modify genetic structure through intense episodes of natural selection (Gutschick and BassiriRad 2003), alter community dynamics, accelerate exotic invasions, and significantly shift vegetation boundaries (Allen and Breshears 1998).

Profound vegetation changes may be imminent in western North America. Hotter, longer summers, higher atmospheric CO_2 levels, and more prevalent extreme events could interact with increasing tree densities and unnatural fuel accumulation to amplify the rates and scales of disturbance, and alter the outcome of succession (Swetnam and Betancourt 1998, Breshears

et al. 2005). Conditions are now ripe for novel invasions from lower elevations, more southerly latitudes, and other continents.

Studies of past extreme climatic episodes and their attendant ecological impacts, including natural invasions, can aid in forecasting ecological changes and developing viable management strategies for western landscapes (Swetnam et al. 1999). Here we offer an example of how paleoenvironmental archives can improve our knowledge of ecological responses to climatic variability and change, particularly during extreme, multidecadal wet–dry cycles that are rarely captured by observational studies. We combine information from fossil woodrat (*Neotoma*) middens and tree rings from Dutch John Mountain (DJM), northeastern Utah, USA (Fig. 1a and b) to examine the potential role of multidecadal climate variability over the past millennium in a range extension of pinyon pine (*Pinus edulis* Engelm.).

METHODS

Study area.—DJM is part of a prominent south-facing sandstone escarpment located on the northeastern slope of the Uinta Mountains in northeastern Utah (Fig. 1a). DJM reaches a maximum elevation of 2312 m, and is broken by Dutch John Gap (1980 m) near its western end. Current vegetation consists of sagebrush steppe and moderately dense (10–20% crown cover) pinyon and juniper (*Juniperus osteosperma* (Torr.) Little) woodlands. Pinyon pine is common on higher slopes (40–95% of woody plant coverage), with Utah juniper and curl-
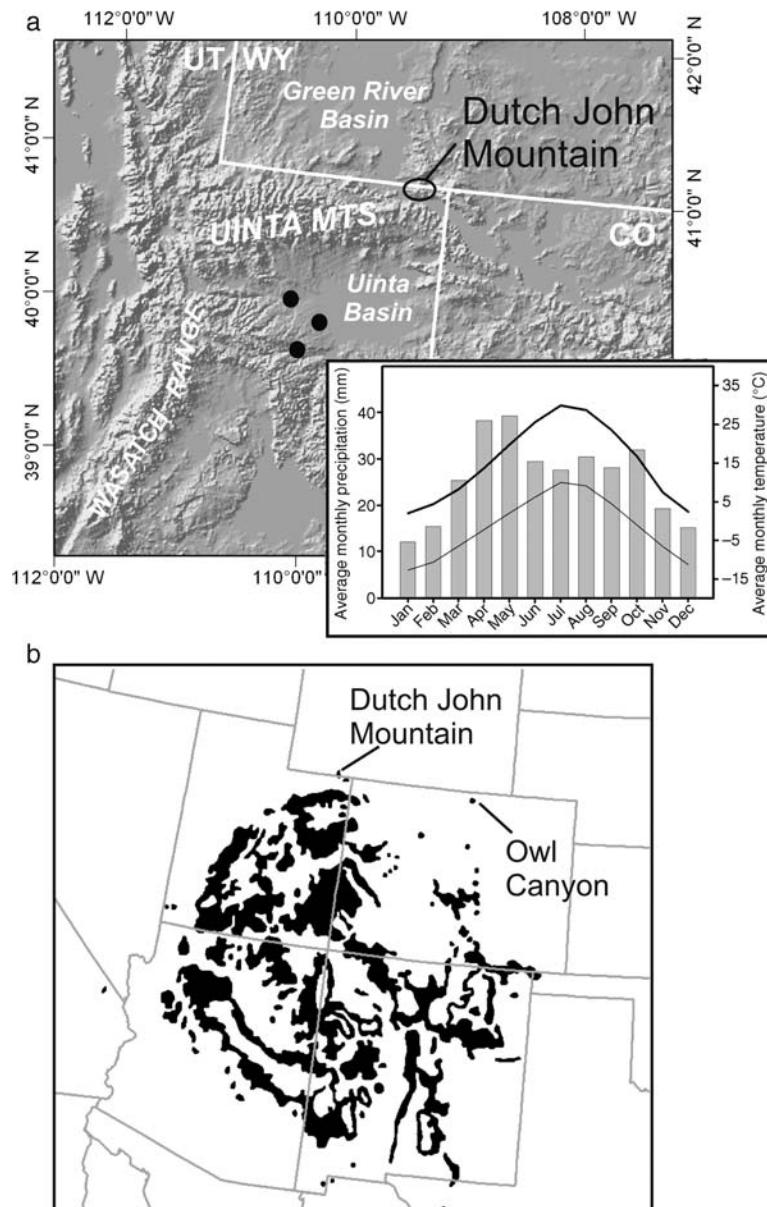
FIG. 1. (a) Shaded relief map showing the location of the Dutch John Mountain study site and tree-ring chronologies (black dots) used in this study. Inset: climograph for the Flaming Gorge meteorological station located 6 km south of Dutch John Mountain showing mean monthly precipitation and temperature for the years 1957–2003 (*data available online*: ⟨http://www.wrcc. dri.edu⟩). (b) Map of Utah, Colorado, Arizona, and New Mexico showing the modern distribution of pinyon pine and the location of the Dutch John Mountain study site.

leaf mountain mahogany (*Cercocarpus ledifolius* Nutt.) as subdominants (up to 30% coverage). Except for scattered individuals a few kilometers from DJM, this site represents the northernmost population of pinyon (Fig. 1b).

Woodrat middens.—We used a series of 60 subfossil woodrat (*Neotoma cinerea*) middens found in rock shelters and crevices along sandstone cliffs to track the development of woodland vegetation at DJM from the late Pleistocene through the Holocene (Jackson et al. 2005). Living pinyons were abundant within woodrat

foraging range ($\sim$50 m) at all of the midden sites. Pollen and macrofossils were extracted from the middens and identified using standard techniques, and the individual middens were dated using ^{14}C methods. Pinyon pine pollen was differentiated from limber pine (*P. flexilis* James) using size criteria (Jackson et al. 2005).

Pinyon pine demography.—As part of an effort to develop tree-ring proxies for precipitation variability in the Uinta Basin Region, Gray et al. (2004) collected cores from 52 pinyons along the south-facing slopes of DJM. For this study, we expanded on Gray et al. (2004) by

systematically sampling for the oldest pinyons on DJM. The site was divided into eight study units, roughly equivalent to the major drainages and topographic features of DJM. We resurveyed six of the study units and cored any additional pinyons showing potential for old age (>500 yr). Two study units not included in the original study were also sampled, and all study units were surveyed for subfossil wood (snags, stumps, and logs from long-dead trees). Age estimates are based on standard cross-dating procedures. Corrections for differences in coring height were made using a regression-derived relationship ($n = 25$, $P < 0.001$, $r^2 = 0.75$) between tree growth and age.

Past climatic variability.—To compare pinyon pine dynamics and climate variability, we reconstructed precipitation from three well-replicated, long-duration (>800 yr) tree-ring chronologies at sites south of the study area (Fig.1a). This reconstruction performs well in the instrumental period ($r^2 = 0.68$), and showed favorable results for calibration and verification tests routinely used in dendroclimatic studies (Gray et al. 2004).

RESULTS

Development of DJM woodlands.—Of the 60 middens collected, 44 encompass the last 12 000 yr (Fig. 2a). Utah juniper first occurred ca. 9485 cal yr BP (calendar years before 1950 based on midden ^{14}C ages), and all younger middens contain abundant Utah juniper macrofossils (see Jackson et al. 2005). Utah juniper, in varied combinations with Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), ponderosa pine (*Pinus ponderosa* P.& C. Lawson), curl-leaf mountain mahogany (*Cercocarpus ledifolius*), and alder-leaf mountain mahogany (*C. montanus* Raf.)*, was the dominant woody plant until pinyon's arrival. Pinyon-type pollen (Fig. 2a) occurs in trace amounts throughout the Holocene, but does not exceed 1% of the pollen sum until 965 cal yr BP (~AD 1080). Pinyon macrofossils first occur in a midden dated to 615 cal yr BP (~AD 1430), coincident with a rise in pinyon-type pollen to >10%. All four middens dating after 615 cal yr BP contain pinyon pine macrofossils (Fig. 2a). From the midden evidence alone, we surmise that pinyon colonized DJM via long-distance dispersal sometime between the 11th and 14th centuries, and subsequently spread to cover and dominate most of the mountain and adjacent canyons of the Green River.

Pinyon pine immigration and expansion.—A group of 33 pinyon individuals, representing the oldest known pinyon at DJM plus the four oldest pinyons from each of the eight study units, indicate the timing and spatial patterns of pinyon colonization and expansion (Fig. 2b). The oldest tree, situated in a shaded alcove near the top of DJM, established in the 13th century (dated to AD 1246). After an interlude of some 70 years, additional pinyon recruitment was recorded at the base of a cliff near the oldest known tree. By the late 14th and early 15th centuries, pinyon pine had reached the lower

slopes. At least one pinyon pine was present on the steep cliffs at Dutch John Gap by AD 1393. Dates from an additional 42 living trees, spread throughout the eight study units and aged >500 yr, show that pinyon was well established throughout DJM by no later than the early 1500s.

Regional climatic variability and woodland dynamics.— The estimated recruitment date of the oldest known pinyon (AD 1246) falls within a period where precipitation was near the long-term mean (19.6 cm; Fig. 2c). The pause in additional invasion and recruitment from AD 1247–1319 coincided with a multidecadal drought, with mean annual precipitation of only 15.1 cm. During the 14th century, a time of rapid pinyon establishment across DJM, annual precipitation rose to 21.1 cm, with several 10-yr periods above 24 cm (i.e., 1330–1339 and 1368–1377; Fig. 2c).

DISCUSSION

Climatic extremes and woodland dynamics.—Pinyon likely colonized DJM from more contiguous and extensive Colorado Plateau populations to the south (Jackson et al. 2005), so the first influx of propagules required a long-distance dispersal event of >40 km. Pinyon seeds are well dispersed by corvids, normally within a few tens of kilometers (Chambers et al. 1999). Pinyon seeds were also a highly valued food among prehistoric peoples who may have played an important role in dispersals of >100 km (Betancourt et al. 1991, 1993).

Pinyon colonization and spread on DJM, and possibly at another isolated outpost in northeastern Colorado (Betancourt et al. 1991), generally coincided with a marked, secular change from the droughty Medieval Warm Period (ca. AD 900-1300) to the wetter Little Ice Age (ca. AD 1300–1850; Fig. 2d) (Cook et al. 2004, Dean 1994). Tree-ring based population histories from stands of ponderosa pine, Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) and pinyon pine indicate widespread vegetation changes in woodlands and forests of the southwestern U.S. and northern Colorado Plateau coincident with the end of the Medieval Warm Period (Swetnam and Betancourt 1998, Swetnam and Brown 1992). As depicted in the midden and tree-ring records, however, development of the pinyon population at DJM was not a smooth, continuous process paced by gradually ameliorating climate. Instead, the progression of pinyon's invasion was markedly episodic. In particular, the tree-ring records show at least one pinyon was present at DJM by the mid 13th century AD, but there are no additional records of recruitment for >70 yr. Beginning in the early 14th century pinyon rapidly colonized the DJM landscape.

These episodic patterns of recruitment could result from natural population processes. More specifically, the first tree-ring date for pinyon might represent an outlier at the end of a long-tailed age distribution. Pinyon snags and logs can, however, be preserved for
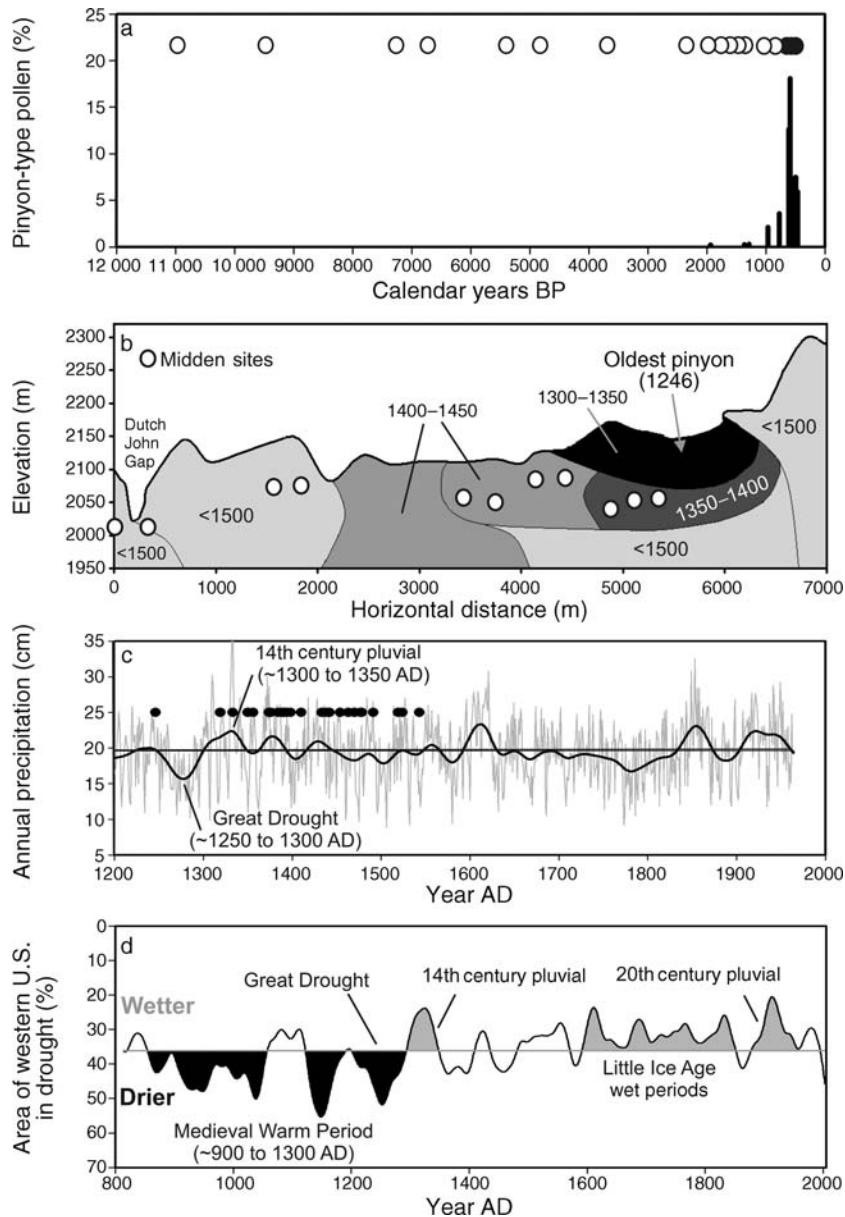
FIG. 2. (a) Percentages of pinyon-type pollen (black vertical bars) and presence (solid circles) or absence (open circles) of pinyon pine macrofossils from 12 000 yr of woodrat (*Neotoma*) midden records collected at Dutch John Mountain (DJM). (b) Profile map of the DJM study area showing locations of midden sites (open circles) and sampling units used in the tree-ring age studies (shaded polygons). Each midden site represents a cave or rock overhang where one or more of the 60 middens were collected. The estimated establishment dates (year AD) are based on the average age of the four oldest pinyon pines found in each sampling unit. (c) Ages for the oldest pinyon tree on DJM and the four oldest pinyons in each of the eight sampling units (black dots) plotted against reconstructed annual (gray line) and 30-yr smoothed (black line) precipitation values for the Uinta Basin Region. (d) Percentage of the western United States experiencing drought conditions over the past 1200 yr as reconstructed from a large tree-ring network (Cook et al. 2004). Data are plotted as a 50-yr moving average. The horizontal line at 37% (dark gray) shows the average or background level of drought through time. Significant multidecadal dry and wet periods identified by Cook et al. (2004) are shaded black and gray, respectively.

many hundreds to thousands of years at similar sites in the region (Gray et al. 2004; C. Baisan, *personal communication*), so some record of additional pinyon recruitment would likely be preserved. Moreover, the presence of Utah junipers more than 800 years old scattered across the site suggests that no stand-replacing

fires occurred on DJM over the past eight centuries or more. The recruitment of this outlier also overlaps with an increase in pinyon-type pollen in the middens, as well as the first occurrence of pinyon macrofossils.

A more compelling explanation for this episodic behavior is found in the progression of strong decadal

wet and dry regimes during the 13th and 14th centuries. The 13th century drought lasted from AD 1250 to 1288, and was the most severe dry period in the region over the past 800 years (Dean 1994, Cook et al. 2004, Gray et al. 2004). Most tree-ring chronologies from western North America spanning this period record a severe multi-decadal drought in the last half of the 13th century (Dean 1994, Woodhouse and Overpeck 1998, Cook et al. 2004), which is also documented by other proxies (e.g., eolian activation records, archeological data). Such a severe dry event limited pinyon's chances for subsequent colonization or spread. Significantly, the 1246 outlier tree survived the drought in one of the most mesic locations on DJM. Abundant soil moisture in the 14th century pluvial period likely promoted pinyon germination and seedling survival.

Though not clear from the available tree-ring and midden records, the 13th century drought might have led to widespread mortality among other woody taxa on DJM, either through direct drought stress or drought-induced disturbances. Such tree and shrub mortality was seen during the less severe 1950s (Betancourt et al. 1993, Allen and Breshears 1998, Swetnam and Betancourt 1998) and 1999–2004 droughts (Breshears et al. 2005). Widespread tree and shrub mortality would have opened favorable microsites for pinyon establishment (Betancourt et al. 1993, Allen and Breshears 1998), promoting rapid pinyon spread and its eventual dominance.

Significant gaps remain in our multiproxy study. In particular, we lack comparable high-resolution information on the dynamics of Utah juniper. In contrast to pinyon, Utah juniper is difficult to age without destructive sampling, and many DJM junipers were hollow, precluding determination of establishment dates. Also, we cannot directly confirm drought-induced mortality of Utah junipers or other woody plants in the 13th century; possible remnants of Utah juniper wood from this event could not be tree-ring dated, and wood from shrubs is generally not preserved for long periods. Decadal-scale climate variability might have also regulated pinyon pine expansion through its effects on seed masting, the abundance and activity of animal dispersers (Chambers et al. 1999), or even the movements of Native Americans (Betancourt et al. 1991, Jackson et al. 2005). To better address such contingencies, a multiproxy approach could be applied across a network of sites in the region. Such a network approach would aid in disentangling the effects of climatic variability from other influences, and would serve to corroborate the limited evidence provided by paleoenvironmental archives from a single site.

Implications for understanding vegetation change.— Long-term ecological dynamics have often been viewed as steady-state processes occurring against a backdrop of randomly fluctuating or gradually changing physical environment. Variations in climate, however, are rarely random or gradual. High-resolution records from tree-rings and other sources indicate that the climate of the past few millennia was characterized by episodic behavior, with variability occurring across a range of temporal scales, and punctuated by regime shifts or abrupt changes from one mode of variability to another (Swetnam and Betancourt 1998, Gray et al. 2003).

Studies of Holocene migration dynamics from throughout North America (e.g., Woods and Davis 1989, Jackson and Booth 2002, Parshall 2002, Lyford et al. 2003) suggest how such climatic variability can influence the progression of migration events. First, climate modulates the frequency of dispersal events and the distances covered. In addition, alternating climatic regimes successively amplify and dampen probability of survival and reproduction after colonization. Shifting climatic regimes may also change the density of favorable habitats for a species across heterogeneous landscapes, and alter competitive interactions and disturbance processes. Most previous studies consider these migrational dynamics over secular to millennial timescales. The work presented here demonstrates that climatic variability over decadal to multidecadal time-scales can produce episodic behavior and spatial complexity in a range expansion. This finding is particularly important given that variability over deca-dal to multidecadal timescales is an especially strong and consistent feature of western North America's climate (Gray et al. 2003), and this inherent behavior is predicted to continue for at least the coming century (Cook et al. 2004).

Most theoretical and analytical models of vegetation change treat climate as a static mean, white-noise process or linear trend, and fail to incorporate episodic variability. This oversight limits our understanding of past vegetation dynamics, and may hinder efforts to forecast future vegetation transitions. Deterministic and statistical biogeographic models, coupled with scenarios of future climate from atmospheric general circulation models, have been widely used to predict the effects of doubled CO_2 on plant species distributions and regional-scale vegetation patterns (e.g., Huntley et al. 1995, Iverson and Prasad 2001, Shafer et al. 2001). In effect, these studies compare a snapshot of instrumental climate and associated vegetation (T_1; Fig. 3a) with a snapshot of modeled future-climate and inferred potential vegetation (T_2). The effects of intervening climatic regimes and their potential ecological impacts are not generally addressed.

If, as suggested by this and other studies, episodic climate variability can influence such processes as disturbance, dispersal, recruitment, mortality, and survival, then the progression, magnitude, and duration of persistent climatic regimes should affect the ecological outcome of climate change. Consider a hypothetical situation where climate is expected to change to a different mean (or variance) in 100 years. Given the impact of inherent multidecadal variability, the inter-vening climate could be realized in multiple ways. In Fig.
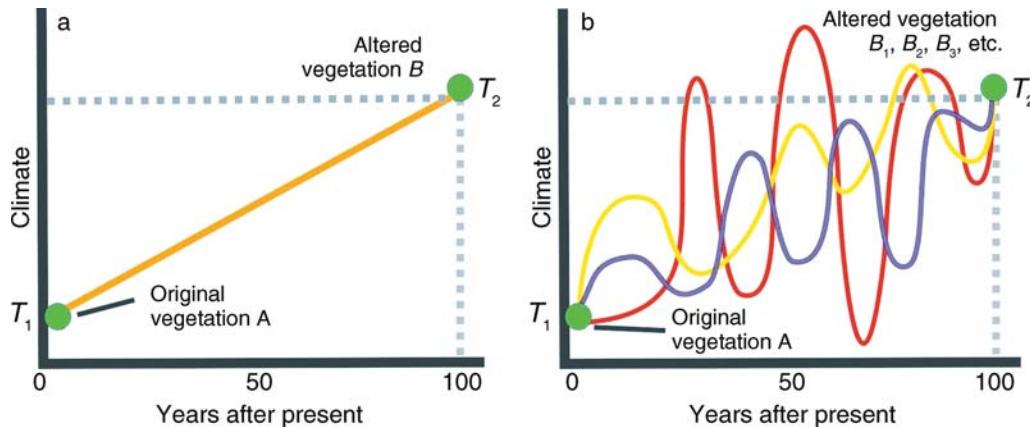
Fig. 3. Conceptual models of future vegetation change driven by (a) secular changes in climate and (b) secular changes in climate combined with decadal to multidecadal climate variability. In (b) the potential outcomes of secular climate change are altered by the legacy of decadal to multidecadal climatic regimes. Even though the same climatic conditions prevail at T_2, when the progression, magnitude, and persistence of climatic regimes vary as shown in the red, blue, and yellow-line scenarios, the potential future vegetation patterns differ as well (i.e., result in alternate vegetation types B_1, B_2, B_3).

3b, three hypothetical versions of intervening climate are presented as the red, yellow and blue traces. The vertical axis in Fig. 3b could represent any climate variable that impacts vegetation structure/composition. If the climate variable in question were moisture stress or temperature, for example, each persistent dry-hot regime depicted in the three scenarios would be accompanied by a high likelihood of disturbances that could disrupt incumbent vegetation, alter resource availability, and perhaps facilitate establishment of novel species. Wet-cool periods would favor rapid recruitment and regeneration. In plant communities dominated by slower growing, long-lived, woody species typical of semiarid regions, the legacy of each of these climatic regimes would then persist on the landscape for many decades or perhaps centuries to come. In the red-line scenario from Fig. 3b high-amplitude swings between persistent dry-hot and wet-cool periods might result in a more vigorous disturbance regime, and therefore greater and more rapid vegetation change, than that in the blue scenario where decadal to multidecadal variability is reduced. Dry-hot and wet-cool regimes of lower magnitude but longer duration depicted in the yellow line scenario might favor the establishment and maintenance of vegetation that approaches equilibrium with climate. As a result, each of the three scenarios for intervening decadal to multidecadal climate variability can produce a different future vegetation condition (e.g., B_1, B_2, and B_3), even with the same climatic conditions at point T_2.

Decadal to multidecadal variability may dampen or amplify the net effects of climatic change associated with the overall trend (Fig. 3b). Because of the additive effects of secular change and decadal to multidecadal variability, the temperature or moisture difference between T_1 and T_2 may be equaled or exceeded for one or more decades over the intervening period. Decadal to multidecadal variability might also result in

a significantly different climate (in terms of its impact on vegetation) being realized well before or after T_2. On the whole, decadal to multidecadal variability increases the range of scenarios for future vegetation change.

Forecast models for plant migration and vegetation change also seldom address the geographic dimensions of episodic climate variability. Growing evidence suggests that most prolonged dry regimes affect large areas of western North America simultaneously (Gray et al. 2003, Cook et al. 2004). Furthermore, the pluvial regimes that often follow such "megadroughts" are equally widespread. This creates a situation where processes taking place at the regional level may also influence landscape dynamics, thus inducing feedbacks between finer and coarser scales and greatly complicating forecasting efforts (Peters et al. 2004). A new generation of models incorporating climate variability and critical processes of range expansion, including dispersal and establishment, is clearly needed. Dynamic global vegetation models (DVGMs) (e.g., Neilson et al. 2005) provide a good starting point, but such models emphasize spatial and not temporal heterogeneity in environment. Incorporation of realistic climate-variability scenarios into DVGMs may provide a more accurate basis for predicting the pattern and pace of species migrations and invasions.

Finally, only two peripheral isolates of *Pinus edulis* (Dutch John Mountain and Owl Canyon, Colorado; Fig. 1a) are known to have originated from long-distance dispersal events within the past millennium. Such founder populations offer model systems for evaluating genetic consequences, intrinsic rates of population growth, local pathways and rates of expansion, and community and ecosystem-level responses associated with plant invasions. In view of accelerated land clearance and climatically driven disturbances, paleoenvironmental archives available at founder sites

should not be taken for granted. Massive quarrying of the local limestone has eroded much of the research potential at Owl Canyon, and in summer 2002 the Mustang Fire destroyed ~10 000 ha of pinyon–juniper woodland, including the oldest pinyon stands, at Dutch John Mountain. The associated loss of scientific resources argue for a regional "salvage paleoecology" initiative in line with the already proposed international effort to rescue critical paleoenvironmental archives at risk of destruction (Alverson et al. 2001).

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