JOURNAL OF QUATERNARY SCIENCE (in press)
Published in 2006 by John Wiley & Sons, Ltd.
Published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/jqs.1023

Inferences about winter temperatures and summer rains from the late Quaternary record of C_4 perennial grasses and C_3 desert shrubs in the northern Chihuahuan Desert†

CAMILLE A. HOLMGREN,[1]* JODI NORRIS[2] and JULIO L. BETANCOURT[3]
[1] Department of Geography, California State University, Long Beach, CA, USA
[2] Department of Botany, University of Wyoming, Laramie, WY, USA
[3] Desert Laboratory, US Geological Survey, Tucson, AZ, USA

Holmgren, C. A., Norris, J. and Betancourt, J. L. Inferences about winter temperatures and summer rains from the late Quaternary record of C_4 perennial grasses and C_3 desert shrubs in the northern Chihuahuan Desert. *J. Quaternary Sci.*, (in press). ISSN 0267-8179.

Received 22 July 2005; Revised 15 February 2006; Accepted 20 February 2006

ABSTRACT: Late Quaternary histories of two North American desert biomes—C_4 grasslands and C_3 shrublands—are poorly known despite their sensitivity and potential value in reconstructing summer rains and winter temperatures. Plant macrofossil assemblages from packrat midden series in the northern Chihuahuan Desert show that C_4 grasses and annuals typical of desert grassland persisted near their present northern limits throughout the last glacial–interglacial cycle. By contrast, key C_3 desert shrubs appeared somewhat abruptly after 5000 cal. yr BP. Bioclimatic envelopes for select C_4 and C_3 species are mapped to interpret the glacial–interglacial persistence of desert grassland and the mid-to-late Holocene expansion of desert shrublands. The envelopes suggest relatively warm Pleistocene temperatures with moist summers allowed for persistence of C_4 grasses, whereas winters were probably too cold (or too wet) for C_3 desert shrubs. Contrary to climate model results, core processes associated with the North American Monsoon and moisture transport to the northern Chihuahuan Desert remained intact throughout the last glacial–interglacial cycle. Mid-latitude effects, however, truncated midsummer (July–August) moisture transport north of 35° N. The sudden expansion of desert shrublands after 5000 cal. yr BP may be a threshold response to warmer winters associated with increasing boreal winter insolation, and enhanced El Niño–Southern Oscillation variability. Published in 2006 by John Wiley & Sons, Ltd.

KEYWORDS: Chihuahuan Desert; bioclimatic envelopes; Pleistocene; Holocene; North American monsoon

Introduction

Despite steady and focused research that now spans half a century, questions linger about the changing seasonality of southwestern USA palaeoclimates. There is general consensus that Late Pleistocene (30 000–13 000 yr BP; all ages are reported in calendar years BP) winters were wetter and temperatures were generally cooler than today (Thompson *et al.*, 1993). The resulting increases in effective moisture permitted large pluvial lakes to grow and persist in what are now dry playas along the Arizona–New Mexico border (Long, 1966; Fleishhauer and Stone, 1982; Waters, 1989; Krider, 1998; Hawley *et al.*, 2000). Increases in effective moisture also supported mixed-conifer forests and open woodlands where there are now pinyon-juniper woodlands, and pinyon-juniper woodlands where there are now deserts (see regional summaries in Van Devender *et al.*, 1987; Betancourt *et al.*, 1990; Thompson *et al.*, 1993; Thompson and Anderson, 2000). Uncertainties remain, however, about the history of summer rains and winter temperatures as could be inferred primarily from biological indicators. In the most recent synthesis of past biomes in western North America based on pollen and packrat midden data, Thompson and Anderson (2000) conclude that the Last Glacial Maximum (ca. 21 000 yr BP) was characterised by (1) southward displacement of the westerlies and enhanced persistence throughout the year; (2) virtual elimination of the present summer monsoon circulation; and (3) a strong temperature gradient throughout the interior, with very cold temperatures to the north and mild conditions along the Mexican border. The dominance of pinyon-juniper woodland species in Pleistocene-aged middens attests to the

*Correspondence to: Camille A. Holmgren, Department of Geography, California State University, Long Beach, 1250 Bellflower Blvd., Long Beach, CA 90840, USA. E-mail: cholmgre@csulb.edu
†This article is a U.S. Government work and is in the public domain in the U.S.A.

importance of enhanced winter precipitation associated with southward displacement of the westerlies and cooler summer temperatures. Here, we aim to refine the latter two inferences by evaluating the packrat midden record and modern bioclimatic distributions of select species in two functional plant groups—C_4 desert grasses and C_3 desert shrubs–that characterise the northern Chihuahuan Desert in the USA–Mexico borderlands (Fig. 1).

The presence and abundance of select C_4 herbs and perennial grasses and C_3 desert shrubs in middens from the northern fringe of the Chihuahuan Desert (Fig. 2), all of which occur today at or near the midden sites, demonstrate interestingly disparate histories. C_4 herbs and grasses persisted from late Pleistocene (Marine Isotope Stages 2 and 3) to the present (MIS 1), whereas many C_3 desert shrubs did not occupy the northern extent of their ranges until the last 4000–5000 years. To evaluate the climatic significance of these patterns, we focused on several C_4 grasses (*Botriochloa barbinodis, Digitaria californica, Leptochloa dubia, Setaria macrostachya*) and C_3 shrubs (*Acacia constricta, Acacia greggii, Flourensia cernua, Fouquieria splendens* and *Larrea tridentata*) common in midden records from the northern Chihuahuan Desert and with easily obtainable distributional data from herbarium collections. We added *Simmondsia chinensis* to the suite of C_3 shrub species because it represents a unique case where a Sonoran Desert species is in the process of invading the northwestern edge (Peloncillo Mts in Figs 1 and 2) of the Chihuahuan Desert. We used distributional data to construct a multidimensional climatic niche for each species, and distances from the niche were calculated and mapped on a 4-km grid for each of 10 climatic variables. The maps are used to evaluate hypotheses about the late Quaternary history of summer rains and winter temperatures in the southwestern United States.

Bioclimatic envelopes

Bioclimatic envelopes can be used to relate physiological functioning of species to conditions found along environmental gradients, such as light, temperature and moisture. The environmental conditions in which a species can survive and reproduce comprise the fundamental ecological niche of a species. Hutchinson (1957) defined the fundamental niche as an *n*-dimensional space consisting of all the environmental conditions within which a species can survive and reproduce. Following Jackson and Overpeck (2000), parts of the fundamental niche can be broken down further into potential and realised niches. Not all climatic combinations occur in nature, so species distributions are limited to areas where the realised environmental variables and the fundamental niche overlap, forming the potential niche space. Within this area of overlap, the species' range may not entirely fill the potential niche if it is limited by other factors such as competition, dispersal ability, etc. As shown in Fig. 3, the realised niche comprises the niche space actually occupied by the species (Jackson and Overpeck, 2000).

The geographic range of a species can be viewed as a spatial reflection of its niche: the species occurs where all environmental conditions are suitable and is absent from areas where one or more conditions are unsuitable (Brown and Lomolino, 1998). Thus, it is possible to re-map distribution patterns from geographic space into climatic space to produce a bioclimatic envelope for a species. We can also map the distance, in terms of climate, that an area falls outside of the bioclimatic envelope to understand potential limiting factors. Once we have constructed present-day bioclimatic envelopes for individual species, the envelopes for assemblages of species found in the fossil record can be determined. The climate at some time in

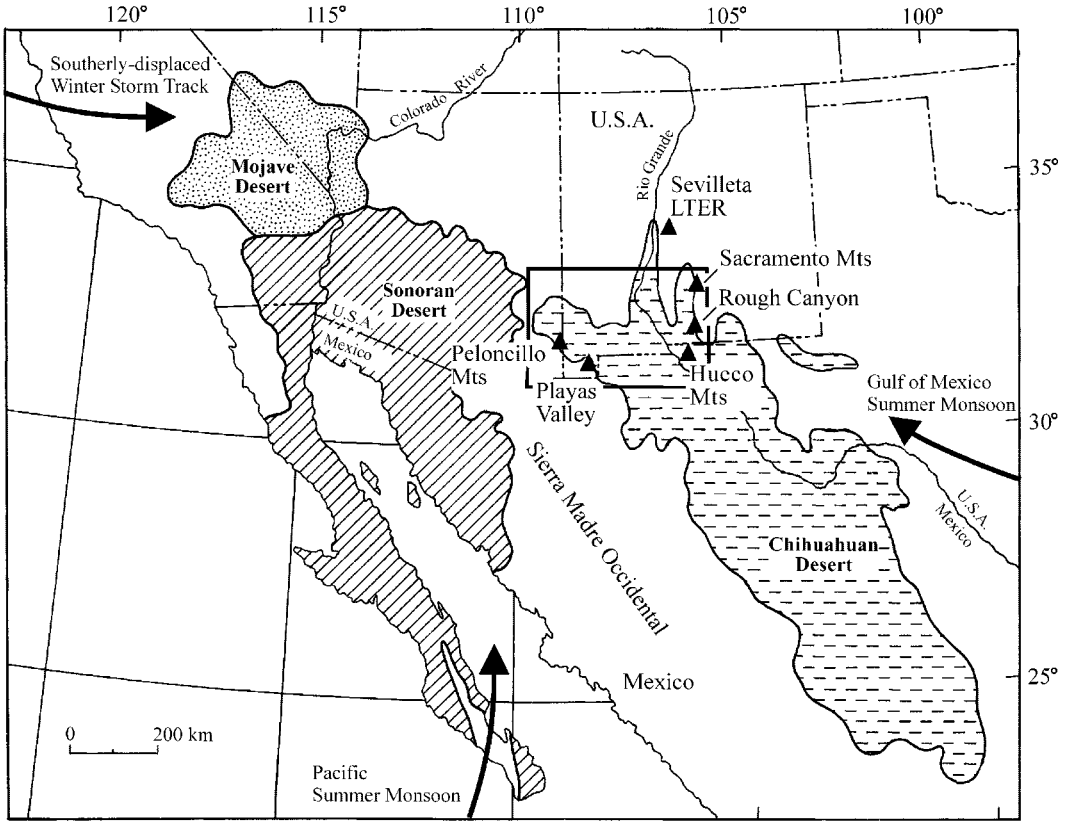

Figure 1 Map of the USA–Mexico borderlands (area in box) with locations of key midden sites (▲) from the northern Chihuahuan Desert. Arrows indicate major moisture sources

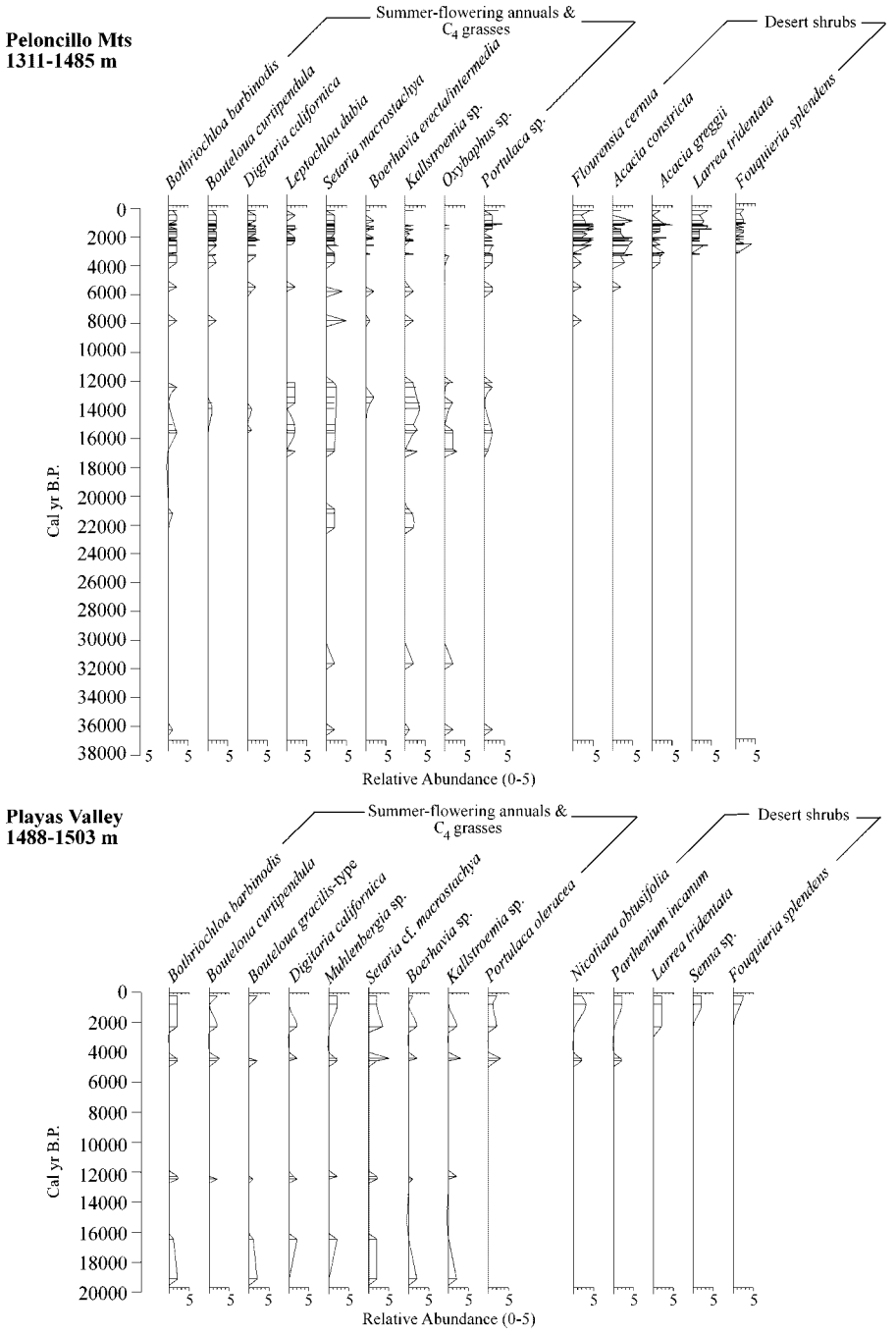

Figure 2 Relative abundance of summer-flowering annuals and C_4 grasses and C_3 desert shrubs through time for sites in the northern Chihuahuan Desert. Note that midden records are discontinuous, with occurrences of midden samples indicated by horizontal bars

the past is inferred to lie within the area of overlap of the climatic ranges for the species present (Atkinson *et al.*, 1986; Elias, 1997).

Two limitations of this technique warrant discussion. First, bioclimatic envelopes produced using geographic ranges are based on realised niches rather than fundamental niches, because non-climatic factors also constrain plant distributions. On smaller spatial scales, non-climatic variables such as topography, canopy cover, soil texture and moisture, nutrient availability, or competitive interactions may be key factors in determining species' distributions. At the continental scale, however, climate is considered the dominant factor regulating plant distribution (Woodward, 1987). In fact, bioclimatic envelopes have been shown to perform well at the macroscale where climatic influences dominate and the impact of biotic interactions is minimised (Pearson *et al.*, 2002; Pearson and Dawson, 2003). A second limitation is the assumption that vegetation, whether today or in the past, is in equilibrium with the contemporary climate. While species ranges continually adjust to both natural and human-induced changes in climate, land use and disturbance, the assumption of equilibrium is probably sound for vegetation on timescales of a few hundred years and longer. Consistent replication in the nature and timing of assemblage changes across remote sites in the same region suggests that, in most cases, this assumption is also valid for the past. Climate models and the fossil record show reasonable agreement between changes in climate and changes in the timing and spatial distribution of vegetation, likewise

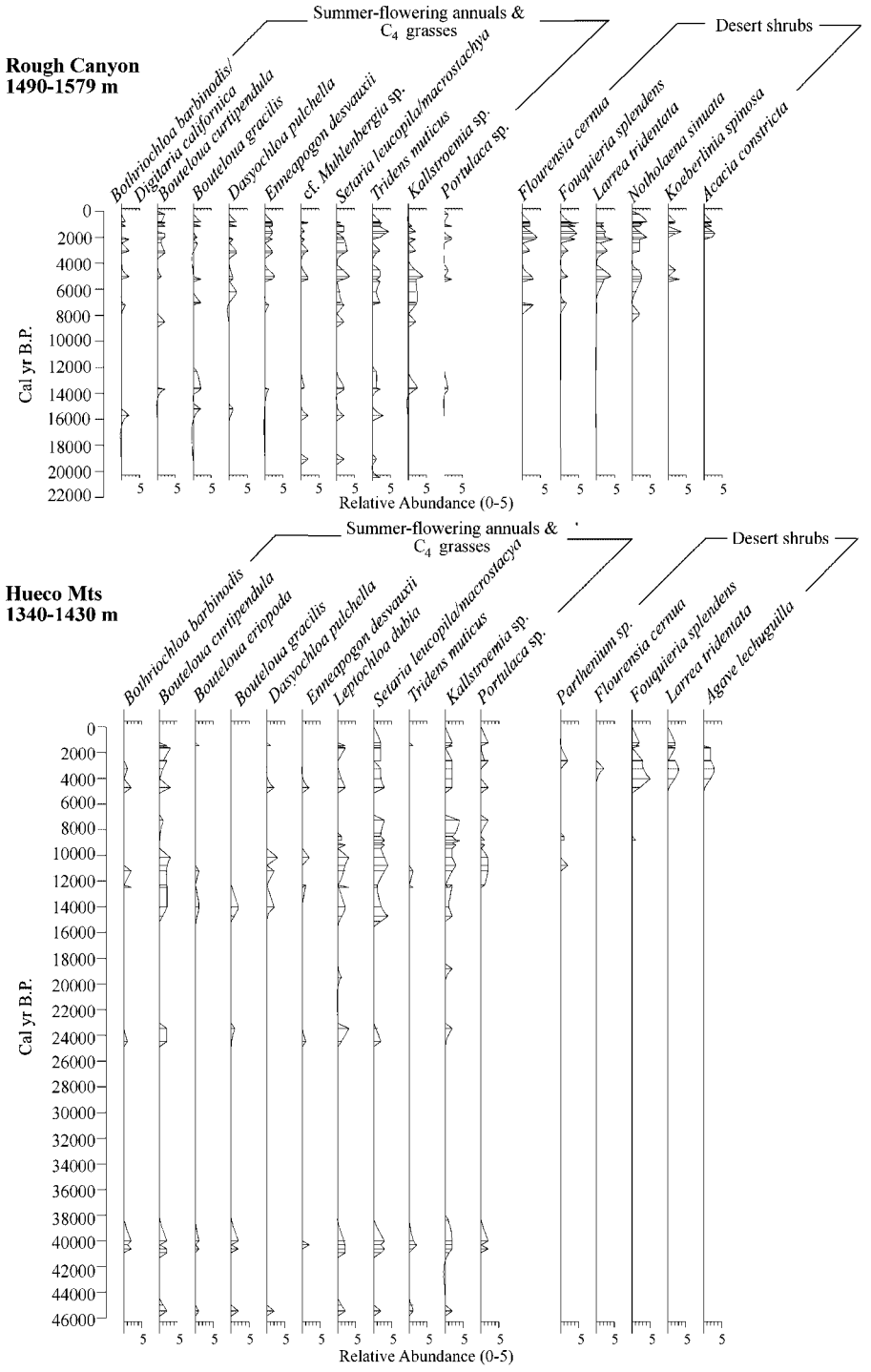

Figure 2 (*Continued*)

supporting the assumption of equilibrium (Williams *et al.*, 2001; Brewer *et al.*, 2002).

The high taxonomic resolution afforded by packrat midden records, where species-level identification of taxa is common, provides a unique opportunity for assessing past climates using information about species' ranges. Bioclimatic envelopes have been used only sparingly, however, to infer climate from packrat midden records (Thompson *et al.*, 1999; Arundel, 2002; Sharpe, 2002; Norris *et al.*, 2006). Here, we used georeferenced herbarium records and a Geographic Information System (GIS)-based approach to construct bioclimatic climatic envelopes for indicator species. Although other platforms such as the GARP modelling system (Genetic Algorithms for Rule-set Prediction; Stockwell and Noble, 1991) improve statistical confidence, the envelope method works well for continuous variables such as climatic data, where range limits represent extremes of tolerance for a species. The envelope method thus allows us to easily extract climatic tolerance data for species to evaluate climatic controls on (1) the relative stability of C_4 grasses and herbs throughout the late Quaternary and (2) the arrival of C_3 desert shrubs in the late Holocene.

Methods

Species presence data for key midden taxa were compiled by integrating georeferenced herbarium data from several different institutions (Table 1). Point-specific data are preferable to

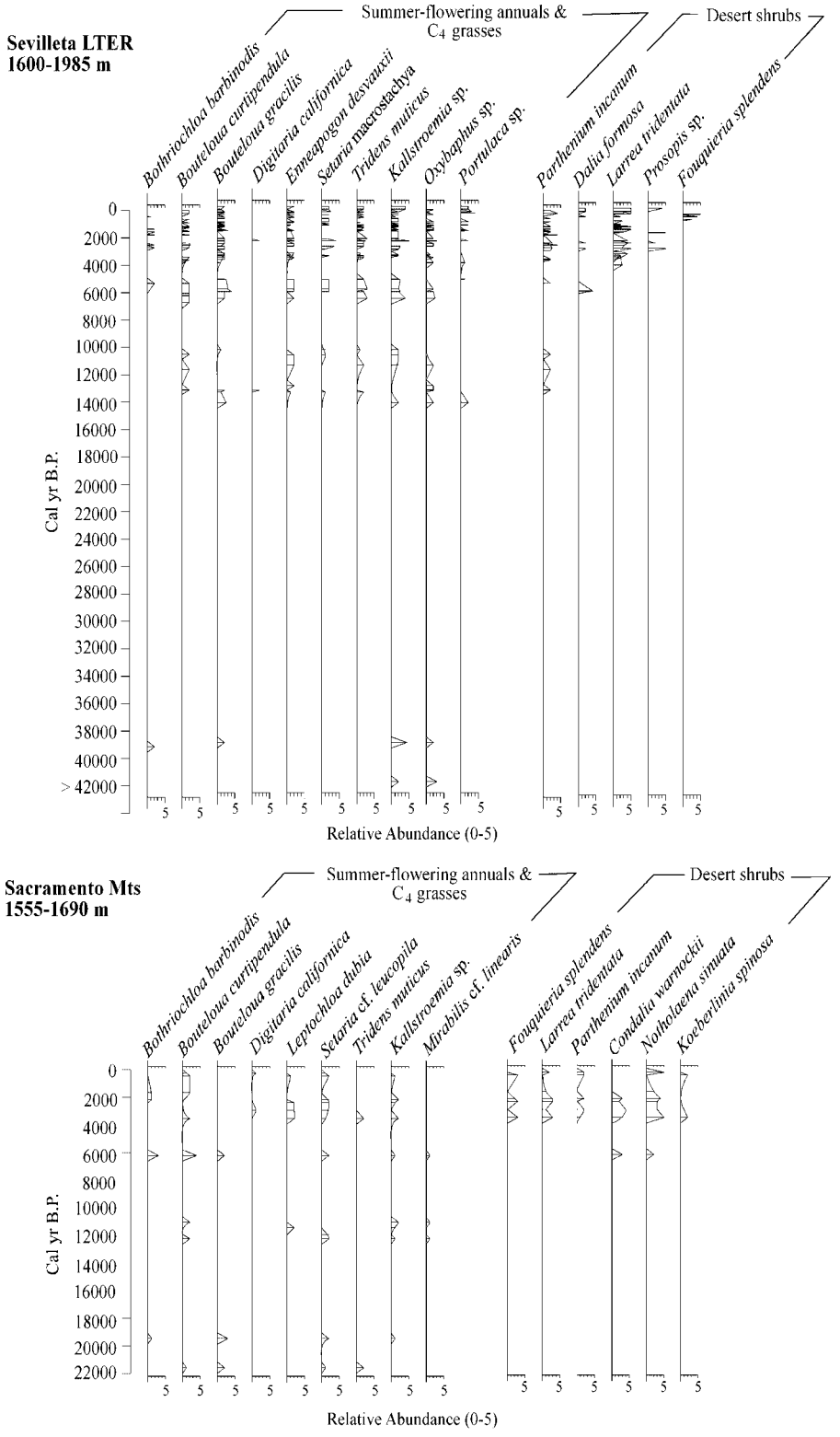

Figure 2 (*Continued*)

generalised (flat) range maps, an important factor when constructing bioclimatic envelopes in mountainous regions where vegetation varies greatly with elevation (Betancourt, 2004). After compiling the database, we removed records that did not contain adequate location data or for which location data were coarser than a minute in latitude/longitude (1.8-km resolution). Any sites were excluded where species were either cultivated or introduced. All latitude–longitude data, as well as township–range–section locations, were standardised to decimal degree. In cases where multiple herbaria records for a species had been collected at a particular site, we removed replicate records. Species occurrence points were then plotted on a base map and any geographic outliers checked for accuracy against location information in the database. Finally, the occurrence data for each species were converted into a separate GIS point coverage.

A grid of climate variables was created from PRISM (Parameter-elevation Regressions on Independent Slopes Model)

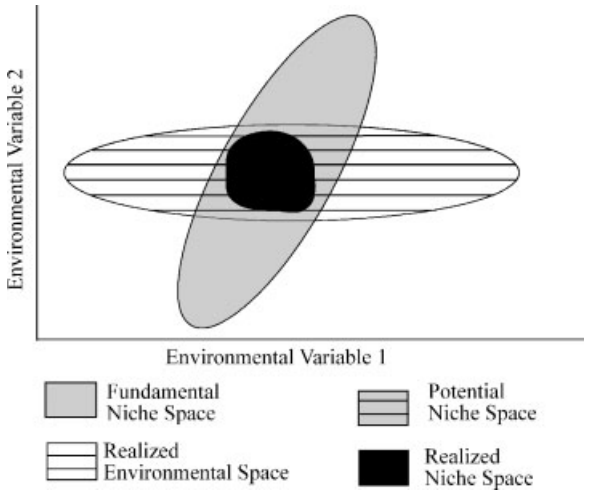

Figure 3 Graphical representation of the fundamental niche space, realised environmental space, potential niche space, and realised niche space. After Jackson and Overpeck (2000)

data (Daly *et al.*, 1997). PRISM uses average climatic values from 1960 to 1990 derived from National Oceanic and Atmospheric Administration (NOAA) weather station data and a moving window of topographically adjusted regression equations to produce 2.5-minute (ca. 4-km) resolution gridded climate data for the western United States (Daly *et al.*, 1997). In other words, the climatic values at each of the grid points represents the climate at the average elevation computed for each grid cell. To create our climate grid, the following variables were selected or derived from PRISM data and overlain in the GIS: mean frost-free period, mean January temperature, mean minimum January temperature, mean July temperature, mean maximum July temperature, mean winter (DJF) precipitation, mean summer (JJA) precipitation, mean growing season precipitation, mean annual precipitation, and summer precipitation/temperature as a measure of heat stress. Because precipitation tends to exhibit a non-normal distribution, we also incorporated grids of logged values for each of the precipitation variables in our climate grid.

Next, we combined the point coverage and climate grid to find the niche space for each species. After joining the point coverage and climate grid, climate data for all variables were extracted at each presence point. Climate data were exported into a spreadsheet and the mean and standard deviation calculated for each variable. All points with values lying outside two standard deviations of the mean for any variable were removed; in the case of precipitation variables, we used the logged variables to trim the data points. We chose to trim the data for several reasons. First, although the PRISM data provide high (ca. 4 km) spatial resolution, we expect that some presence points occur at much lower/higher elevation than the average elevation of grid cells that encompass a broad range of elevations. Second, species occurrence data may contain inaccuracies due to poor initial field location determinations, errors in estimation of latitude and longitude from township–range–section data, or database errors. Removing points that fall outside of two standard deviations should minimise these types of errors. In addition, with few exceptions, visual inspection of the niche spaces created with the trimmed data compared more favourably with known distributions than those created using untrimmed data. After trimming the data, we selected only those cells where climatic conditions fell within the trimmed minimum and maximum values to construct the niche space. For points falling outside of the niche space, we calculated the distance, in terms of climate, from the niche space for each variable. In the case of precipitation variables, we calculated distances using the non-logged values to facilitate interpretation.

Table 1 List of herbarium data souces

Institution	Herbarium code
Arizona	
Arizona State University	ASU
Desert Botanical Garden	DES
Northern Arizona University	ASC
University of Arizona	ARIZ
SALVIAS	
California	
Rancho Santa Ana Botanical Garden	RSA
University of California at Berkeley	UC, JEPS
University of California at Riverside	
Colorado	
Colorado State University	CS
University of Colorado	COLO
Kansas	
University of Kansas Natural History Museum	KANU
Mexico	
Instituto de Ecologia, A.C.	IEB
Missouri	
Missouri Botanical Garden	MO
Nebraska	
University of Nebraska at Omaha	OMA
University of Nebraska State Museum	NEB
Nevada	
University of Nevada at Las Vegas	UNLV
University of Nevada at Reno	RENO
New Mexico	
New Mexico State University	NMC, NMCR
University of New Mexico	UNM
Texas	
Angelo State University	SAT
Sam Houston State University	SHST
Southwest Texas State University	SWT
Stephen F. Austin State University	ASTC
Texas A&M University	TAES, TAMU
University of Texas at Austin	LL, TEX
West Texas A&M University	WTS
Utah	
University of Utah	UT
Utah State University	UTC

Results

Species presence points versus the modelled niche space

Figure 4 shows species presence points versus the modelled niche space for all species. Points falling outside of the modelled niche space are the trimmed points, i.e. those that exceeded the 2-σ range for one or more variables. The modelled niche space extending beyond the presence points represents potential niche space for the species. Again, one possible source of error derives from the fact that the climatic values for each point used to construct the niche space represent climate at the average elevation for the grid cell, which may be higher or lower than the actual elevation. Even so, this technique is a significant improvement over the use of flat range maps that are not elevation-specific, and good agreement exists between the modelled niches and known distributional data (i.e. Turner

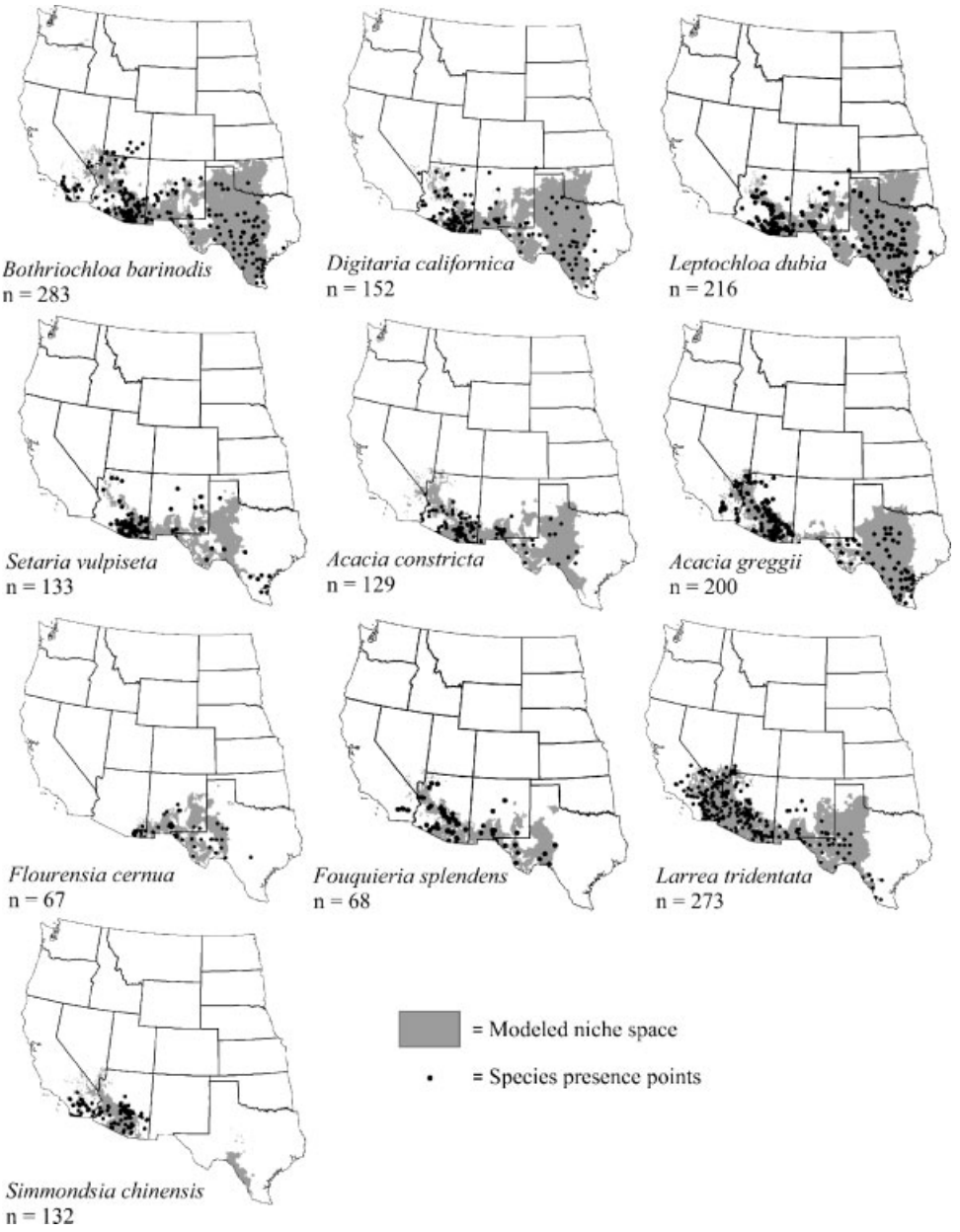

Figure 4 Comparison of species point-occurrences from herbarium data and modelled niche space

et al. (1995), although this work does not extend east of the Arizona–New Mexico border) suggests error is minimal.

Climatic envelopes for C_4 grasses

The climatic controls on the distribution of the C_4 grasses *Bothriochloa barbinodis, Digitaria californica, Leptochloa dubia* and *Setaria macrostachya* are apparent in Figs 5–8. The northern limits for these species are strongly influenced by mean January temperature, mean minimum January temperature, and frost-free period, with mean January temperature having an effect over the greatest spatial extent. We expect these variables to be highly correlated since areas with colder mean January temperatures are also likely to have colder minimum temperatures and a shorter frost-free period. Cold summers (mean July temperature, mean maximum July temperature) also appear to be limiting north of the physiographic break that separates the low, warm deserts from the higher, colder ones to the north (the Great Basin and Colorado Plateau). Lowlands in the basins and valleys to the north, however, are apparently warm enough in the summer but too cold in the winter for these desert grassland species. The latter may be due to the large temperature inversions in winter that characterise the Colorado Plateau and Great Basin (Whiteman *et al.*, 1999).

Summer (JJA) precipitation and growing season precipitation are the main limiting factors to the west, although these are somewhat less important for *Bothriochloa barbinodis* than the other grasses (Fig. 5). During summer, high temperatures also restrict the presence of these C_4 grasses in southwestern Arizona and southeastern California. The combined influence of high summer temperatures and moisture deficit is notable in the map of heat stress (summer precipitation/temperature). Conversely, maps of mean annual precipitation, growing season precipitation, and summer precipitation/temperature indicate that conditions to the east are too wet.

A comparison of the bioclimatic envelopes produced for 21 170, 15 410, 13 925 and 12 405 yr BP at the Peloncillo Mountains Wilderness Area (PMWA) site allows us to place

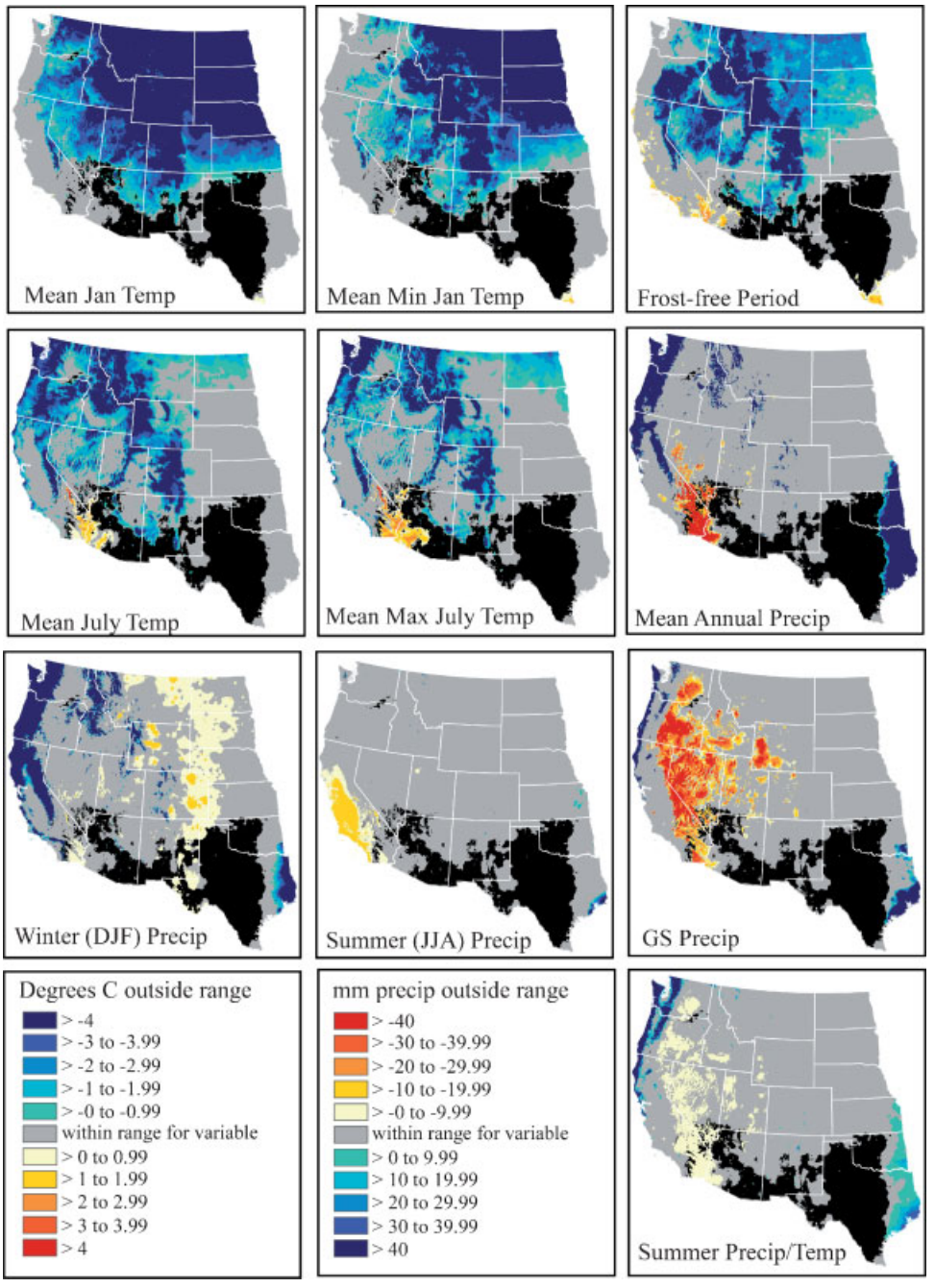

Figure 5 Niche space for C_4 *Bothriochloa barbinodis* (shown in black) with the distance from the niche space for 10 variables. For Figures 3–14, the area in grey indicates the area outside of the niche space when all variables are considered, but within the potential niche space for a particular variable

boundaries on the Late Pleistocene climatic conditions in the northern Chihuahuan Desert. For each period examined, we compare only those species that appear in the midden record at that time. Assuming that the climatic tolerances of individual species have not changed over time, using only the species present allows us to simulate assemblages for which there may be no modern analogue. Climatic range limits for each species were determined from bioclimatic envelopes (Table 2), and the lower range limits for species present at various time periods were subtracted from the modern values for mean January temperature (6.9 °C), mean July temperature (27.7 °C), and mean summer precipitation (105.5 mm). For 21 170 yr BP during the Last Glacial Maximum, our results indicate that mean January temperatures were not below 2.4 °C (4.5 °C lower than today) and mean July temperatures were not below 23.3 °C (4.4 °C lower than today), while mean summer precipitation was *at least* 80 mm. For 15 410, 13 925 and 12 405 yr BP, mean January and July temperatures remained the same, but modelled mean summer precipitation was 105.3 mm, which is equivalent to modern summer precipitation along the Arizona–New Mexico–Mexico border. The summer precipitation value of 105.2 mm is based on the niche requirements for *Leptochloa dubia* and is significantly greater than the amount for other species, which have minimum summer precipitation values between 55.1 and 80.1 mm.

C_3 desert shrubs

The bioclimatic envelopes for all desert shrub species studied (*Acacia constricta, Acacia greggii, Flourensia cernua,*

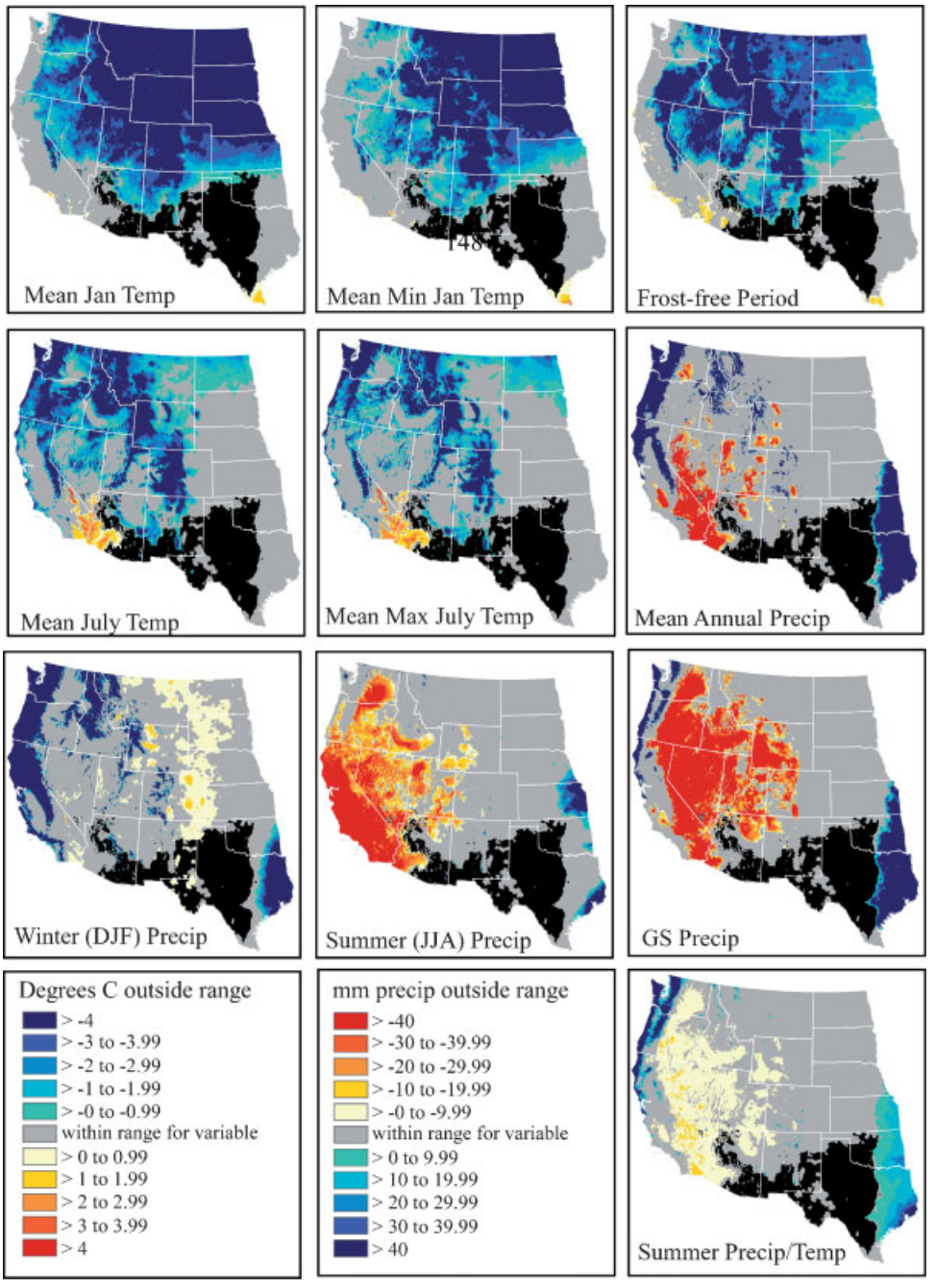

Figure 6 Niche space for C_4 *Digitaria californica*

Fouquieria splendens, Larrea tridentata and *Simmondsia chinensis*) are remarkably similar (Figs 9–14). To the north, cold mean January temperature, cold mean minimum January temperature, and a short frost-free period strongly limit the niches of all species. Cold mean July temperature and mean maximum July temperatures also appear limiting to the north, but less so than winter temperatures. To the west, hot and dry summer conditions (summer precipitation, growing season precipitation, summer precipitation/temperature, mean July temperature, and mean maximum July temperature) truncate the niches for most species. An exception is *Larrea tridentata,* which is excluded only from lower Colorado Delta vicinity and southwestern California and appears more tolerant of hot, arid conditions. In the east, wetter conditions in central and eastern Texas fall outside the climatic range for all species.

Comparison of bioclimatic envelopes for desert shrub species in the PMWA shows a warming trend in winter temperatures in the mid- to late Holocene. The presence of *Flourensia cernua* and *Acacia constricta* by 5460 yr BP indicates that mean January temperatures were not below ca. 3 °C (i.e. ca. 4 °C cooler than today). The arrival of *Acacia greggii* by 3760 yr BP suggests mean January temperatures had warmed another ca. 0.5 °C. Establishment of the disjunct population of *Simmondsia chinensis,* the most cold-intolerant species with a mean January temperature of 6.38 °C (only 0.5 °C cooler than today), in the PMWA between ca. 2260–0 yr BP (Holmgren *et al.*, in press) indicates further warming of winter temperatures. Although the arrival of desert shrubs is a notable occurrence throughout the northern Chihuahuan Desert during the latter part of the mid-Holocene, there is no obvious sequence of species arrivals. It is clear that other factors such as dispersal ability, distance from late glacial refugia, or other climatic, biotic or edaphic variables can factor into species arrival times.

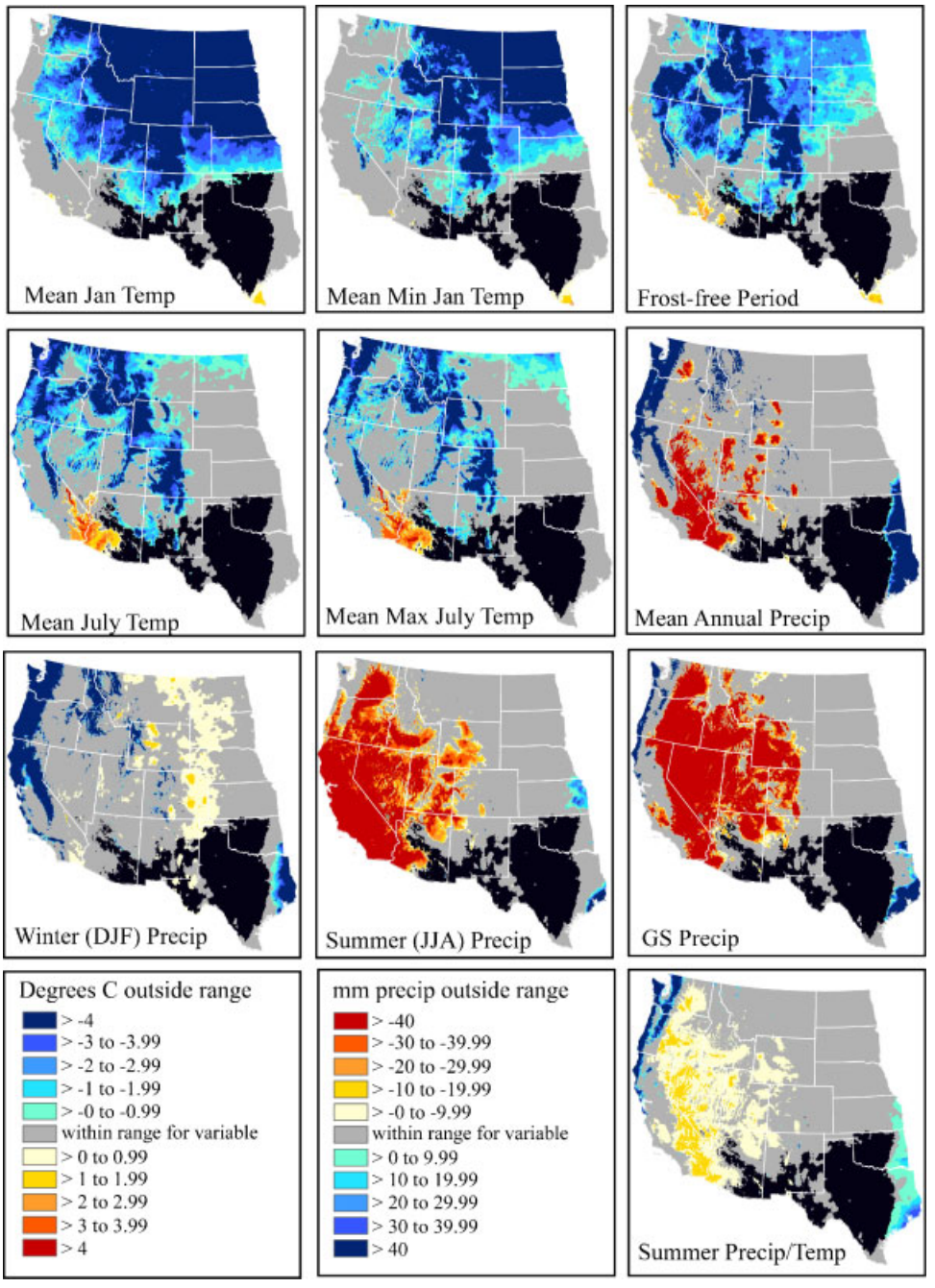

Figure 7 Niche space for C_4 *Leptochloa dubia*. This figure is available in colour online at www.interscience.wiley.com/journal/jqs

Discussion

We have considered the large-scale climatic factors limiting modern species distributions in order to understand climatic controls on Late Pleistocene and Holocene vegetation in the northern Chihuahuan Desert. Our analysis is based on correlations among species distributions and climatic variables, and as such, we cannot establish causal relationships. Because autecological and physiological information is incomplete for all of the selected species, our models are by necessity statistical and not deterministic. The similarity of the limiting factors identified for related plant functional types (perennial C_4 grasses, desert shrubs), however, lends credence to their importance in influencing plant distributions.

Late Pleistocene climate

The presence of C_4 herbs and grasses in late Pleistocene middens from the Bolson de Mapimi (ca. 26–27 ° N) in Mexico and Big Bend (ca. 29 ° N) in Texas to the Tularosa Basin (32–33 ° N), southern New Mexico was long noted by Van Devender (Van Devender and Riskind, 1979; Van Devender *et al.*, 1984; Van Devender and Burgess, 1985; Van Devender and Toolin, 1983; Van Devender, 1990; Van Devender, 1995). The prevalence of these summer-flowering species throughout the last 40 000 years has been confirmed for the Tularosa Basin (Betancourt *et al.*, 2001), the middle Rio Grande Valley south of Albuquerque (Betancourt, Rylander and Anderson, in prep.), and Playas (Holmgren *et al.*, 2003) and San Simon valleys (Holmgren *et al.*, in press) of southwestern New Mexico and southeastern Arizona, respectively (Fig. 2). Recent work integrating carbon

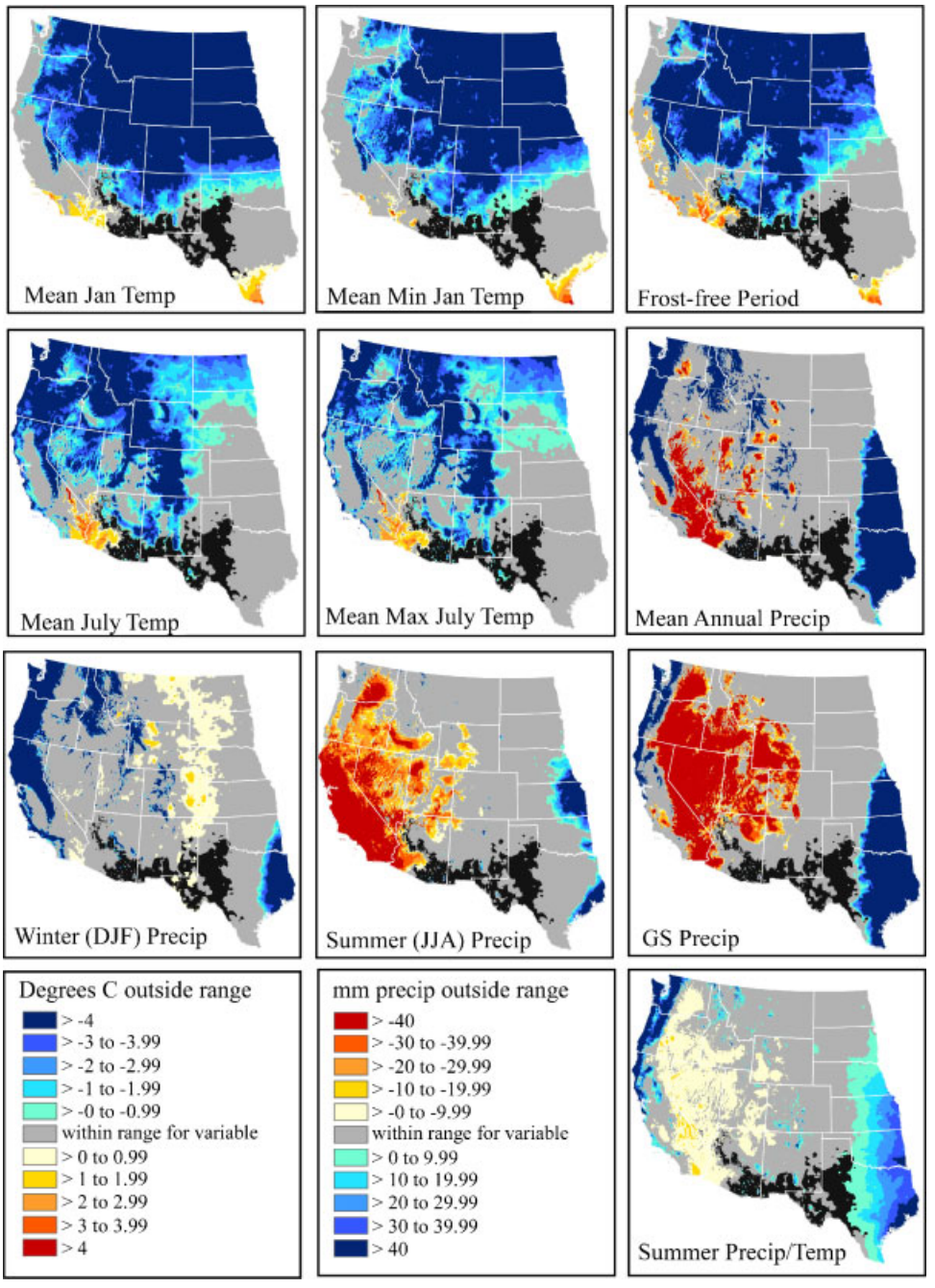

Figure 8 Niche space for C_4 *Setaria macrostachya*. This figure is available in colour online at www.interscience.wiley.com/journal/jqs

isotopes from soil carbonates (Liu *et al.*, 1996; Monger *et al.*, 1998) and tooth enamel from megaherbivores (Connin *et al.*, 1998; Koch *et al.*, 2004) suggests that the C_4 grass occurrences represent more than just secondary elements in woodland understories. Instead, they were part of an expansive summer-flowering C_4 grassland that stretched from central Texas to southern Arizona, mostly south of 35° N. These may have been the northernmost grasslands in western North America to green up in response to mid-to-late summer rains during the glacial period. Although some C_4 grass species may respond opportunistically to available moisture regardless of season (Van Devender 1990), this argument is less likely to apply to the diverse suite of C_4 grasses and summer-flowering annuals identified from Pleistocene middens. Surprisingly, many of the C_4 grasses (e.g. *Botriochloa barbinodis, Digitaria californica, Leptochloa dubia, Setaria macrostachya*) that appear in the Late Pleistocene midden record of the northern Chihuahuan Desert do not extend much further north today, and thus can help constrain the magnitude of glacial-age cooling.

The results of our bioclimatic envelopes suggest cold winter temperatures are an important factor limiting the distribution of many C_4 grass species along their northern and upper elevation range margins. There is currently little consensus, however, regarding physiological constraints on C_4 plant distribution in cold climates. Dissociation of the C_4 enzymes pyruvate-phosphate dikinase and PEP carboxylase (Long, 1983; Potvin *et al.*, 1986), Rubisco limitation (Long 1999; Kubien *et al.*, 2003), and lower quantum yield of C_4 versus C_3 grasses (Ehleringer *et al.*, 1997) at lower temperatures have all been proposed as explanations for the scarcity of C_4 species in cold environments. Most of these studies have focused on low temperatures during

Table 2 Table of climatic ranges from bioclimatic envelopes

	Winter (DJF) Precip. (mm)	Frost-free period (Days)	Growing season Precip. (mm)	Summer (JJA) precip. (mm)	Summer precip. temp.	Annual precip. (mm)	Mean Jan. temp. (°C)	Mean min. Jan. temp. (°C)	Mean July temp. (°C)	Mean max. July temp. (°C)
Bothriochloa barbinodis	32.38–238.23	170–364	107.18–867.33	18.02–344.58	11.42–78.64	162.88–934.53	0.63–13.87	−7.47–8.10	21.25–32.61	29.16–39.57
Digitaria california	34.39–176.16	173–361	173.83–693.37	68.42–316.75	17.00–66.79	216.43–865.15	1.98–12.81	−6.49–7.56	21.73–32.62	29.33–40.64
Leptochloa dubia	32.38–234.04	180–352	193.98–887.48	105.34–286.55	19.24–80.54	248.51–1064.78	2.07–13.10	−6.22–7.66	22.22–30.72	29.57–38.04
Setaria vulpiseta	31.23–176.16	196–330	166.40–540.2	80.7–260.46	16.39–47.77	229.84–668.29	2.40–11.02	−5.22–5.15	23.32–31.30	31.10–39.29
Acacia constricta	31.15–164.78	190–356	124.26–554.51	32.77–277.51	12.12–53.93	151.71–682.09	2.94–12.43	−6.22–6.56	22.59–33.70	30.56–40.79
Acacia greggii	32.38–200.10	209–358	107.66–794.19	29.20–277.51	9.00–71.77	126.04–882.34	3.48–13.10	−3.92–7.66	24.17–34.14	31.41–41.71
Flourensia cernua	31.15–82.06	185–274	184.8–453.59	105.31–203.71	19.72–43.21	241.75–528.68	1.79–8.29	−6.44–1.85	22.45–28.77	30.41–37.07
Fouquieria splendens	32.38–180.35	190–364	150.48–473.62	44.33–234.95	13.17–44.28	178–7–552.15	3.26–12.23	−6.22–6.44	23.71–32.86	31.05–40.90
Larrea tridentata	24.96–167.08	184–364	66.93–553.53	8.96–277.51	5.54–53.01	73.19–637.90	3.05–13.05	−4.75–7.74	23.19–35.87	30.57–42.76
Simmondsia chinensis	40.62–216.08	246–364	96.24–531.50	15.48–277.51	9.16–53.01	133.12–637.90	6.38–12.83	−1.53–7.59	24.40–34.90	31.76–42.21

the growing season, but our results suggest that winter temperatures may be equally important in limiting C_4 grasses. Some C_4 species can tolerate cold temperatures when dormant (Schwarz and Reaney, 1989) and during the growing season (Sage and Sage, 2002), but a late hard freeze after germination may limit establishment by impacting the chilling-susceptible seedlings in many species. For example, *Zea mays* exhibits loss of photosynthetic capacity due to photoinhibition during periods of high light intensity and low temperatures. Seedlings may be especially vulnerable to light-dependent damage because they emerge when periods of low chilling temperatures coincide with high light levels (Long, 1983, 1999). Although we currently cannot resolve the physiological basis for limited C_4 grass distribution in cold climates, the presence of C_4 grasses in Late Pleistocene middens nevertheless provides evidence for relatively mild winter temperatures. Continued investigation of the role of cold winter temperatures and length of frost-free period is warranted.

Reconstructed summer temperatures during the Late Pleistocene were also cooler than modern, although the amount of cooling is uncertain. C_4 grass bioclimatic envelopes indicate mean July temperature was no more than 5.5 °C cooler than today. However, this low temperature limit may have been altered during the Late Pleistocene owing to shifts in dominance between C_3 and C_4 species. The higher quantum yield of C_3 species at low temperatures may limit C_4 grass distribution at sites with cooler growing season temperatures via competitive exclusion (Ehleringer *et al.*, 1997). During the Late Pleistocene, however, C_4 photosynthesis may have been favoured at lower summer temperatures when reduced crossover temperatures (the mean monthly temperature at which C_4 plants have a higher quantum yield than C_3 plants) resulted from decreased atmospheric CO_2 concentration (Ehleringer *et al.*, 1997; Koch *et al.*, 2004). Thus, minimum summer temperatures for C_4 grasses may have been more than 5.5 °C cooler during the Late Pleistocene, assuming that low summer temperatures are regulated via competition with C_3 species rather than other physiological mechanisms. In contrast, changes in crossover temperatures would have had negligible effects in winter when C_4 grasses are inactive.

Bioclimatic envelopes also allow us to quantify the amount of Late Pleistocene summer precipitation in the borderlands. The opportunity for assessing the seasonality of precipitation changes, a rare opportunity in proxy records, is possible due to the high taxonomic resolution afforded by packrat midden records where species-level identifications are common. The importance of summer precipitation in the borderlands was inferred previously from the diverse suite of C_4 grasses and summer-flowering annuals found in glacial-aged packrat middens (Betancourt *et al.*, 2001; Holmgren *et al.*, 2003, in press), although the amount of summer precipitation was unknown. We now estimate that summer precipitation was equivalent to at least 50% of modern values and may have reached amounts similar to today.

In contrast to models suggesting the virtual elimination of summer monsoonal precipitation (Thompson and Anderson, 2000), we find that at least moderate amounts of summer precipitation characterised Late Pleistocene climate in what is now the northern fringe of the Chihuahuan Desert. Note that we do not imply a diminished role for winter precipitation during the Late Pleistocene, because greater-than-present winter precipitation is still necessary to account for the increased effective moisture needed to fill pluvial lakes and support displacement of woody C_3 highland species into the lowlands. Rather, we suggest that summer precipitation was more extensive in the USA–Mexico borderlands than previously thought. Thus, it appears that key atmospheric and topographic features

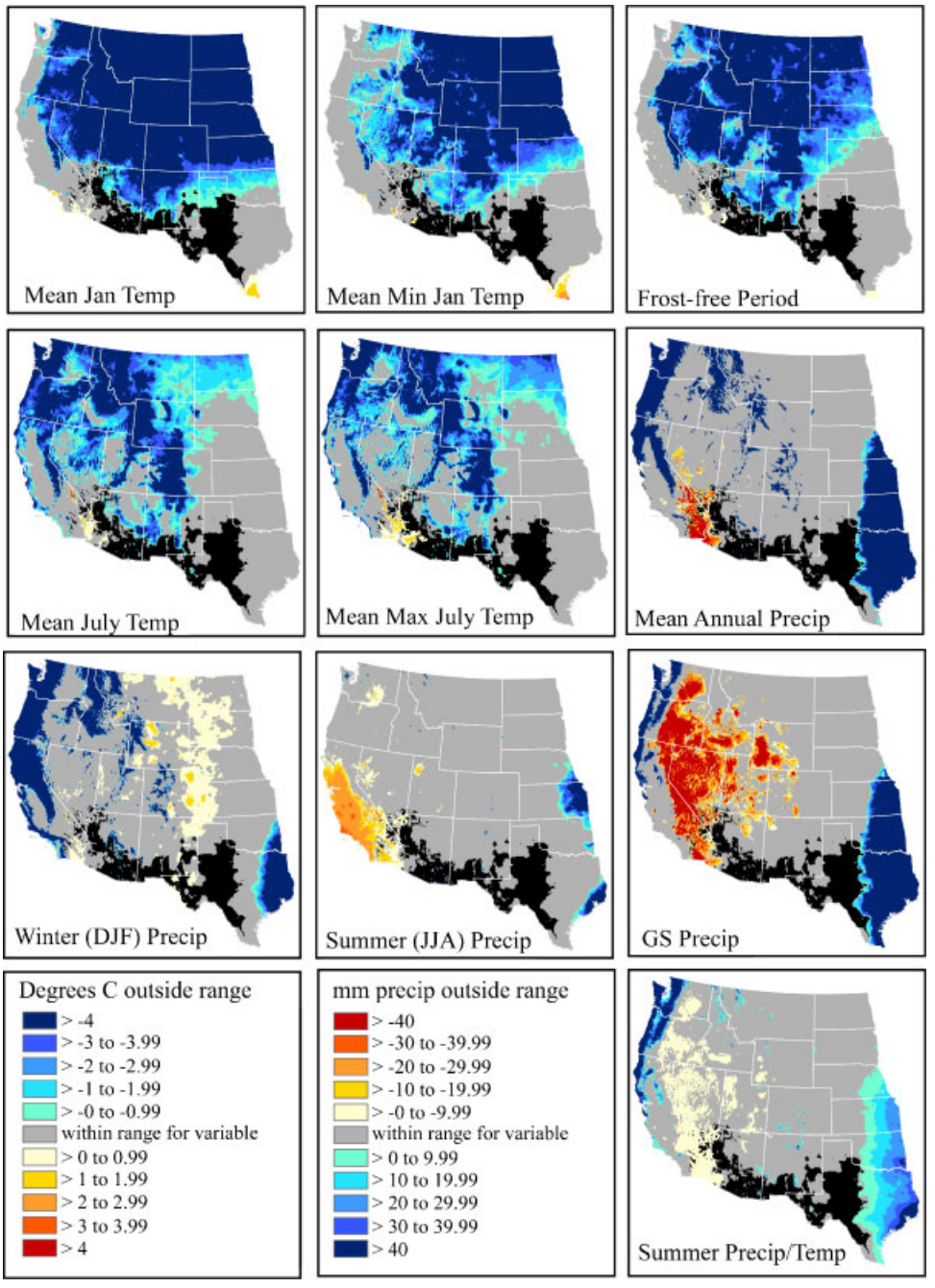

Figure 9 Niche space for C_3 *Acacia constricta*. This figure is available in colour online at www.interscience.wiley.com/journal/jqs

anchoring the core of the North American monsoon over the Sierra Madre Occidental in Mexico and the tongue of moisture extending northward to the Arizona–New Mexico border remained intact during the glacial period. Although we cannot resolve the relative contributions of the eastern Pacific–Gulf of California and Gulf of Mexico to Late Pleistocene summer precipitation, both are generally viewed as important moisture sources for the North American monsoon with low-level moisture primarily derived from the Gulf of California and upper-level water vapour coming from the Gulf of Mexico (Stensrud *et al.*, 1995; Schmitz and Mullen, 1996; Adams and Comrie, 1997). In the mid-latitudes, on the other hand, persistent snowpack and southward displacement of the westerlies may have curtailed monsoonal precipitation to the north, as indicated by the scarcity of C_4 grasses and annuals in midden records from the Colorado Plateau (Betancourt, 1984, 1990).

In contrast to C_4 grasses, C_3 desert shrubs remained absent from the USA–Mexico borderlands during the Late Pleistocene. Although the northern limits of C_3 desert shrub are similar to those of C_4 grasses, their absence during the Late Pleistocene may have been due to the somewhat higher minimum winter temperature requirements. Both low mean January temperatures and mean minimum January temperatures for desert shrub species are generally higher than those for C_4 grasses (1.79 to 6.38 °C vs. 0.63 to 2.40 °C and −6.44 to −1.53 °C vs. −7.47 to −5.22 °C, respectively), which may have been sufficient to exclude them during the Late Pleistocene. Alternatively, wetter Late Pleistocene conditions may have prevented the establishment of desert shrub species via competitive exclusion by more mesic-adapted species. Whatever the case, the majority of desert shrubs species remained notably absent from the northern Chihuahuan Desert prior to their abrupt arrival around 5000–4000 yr BP.

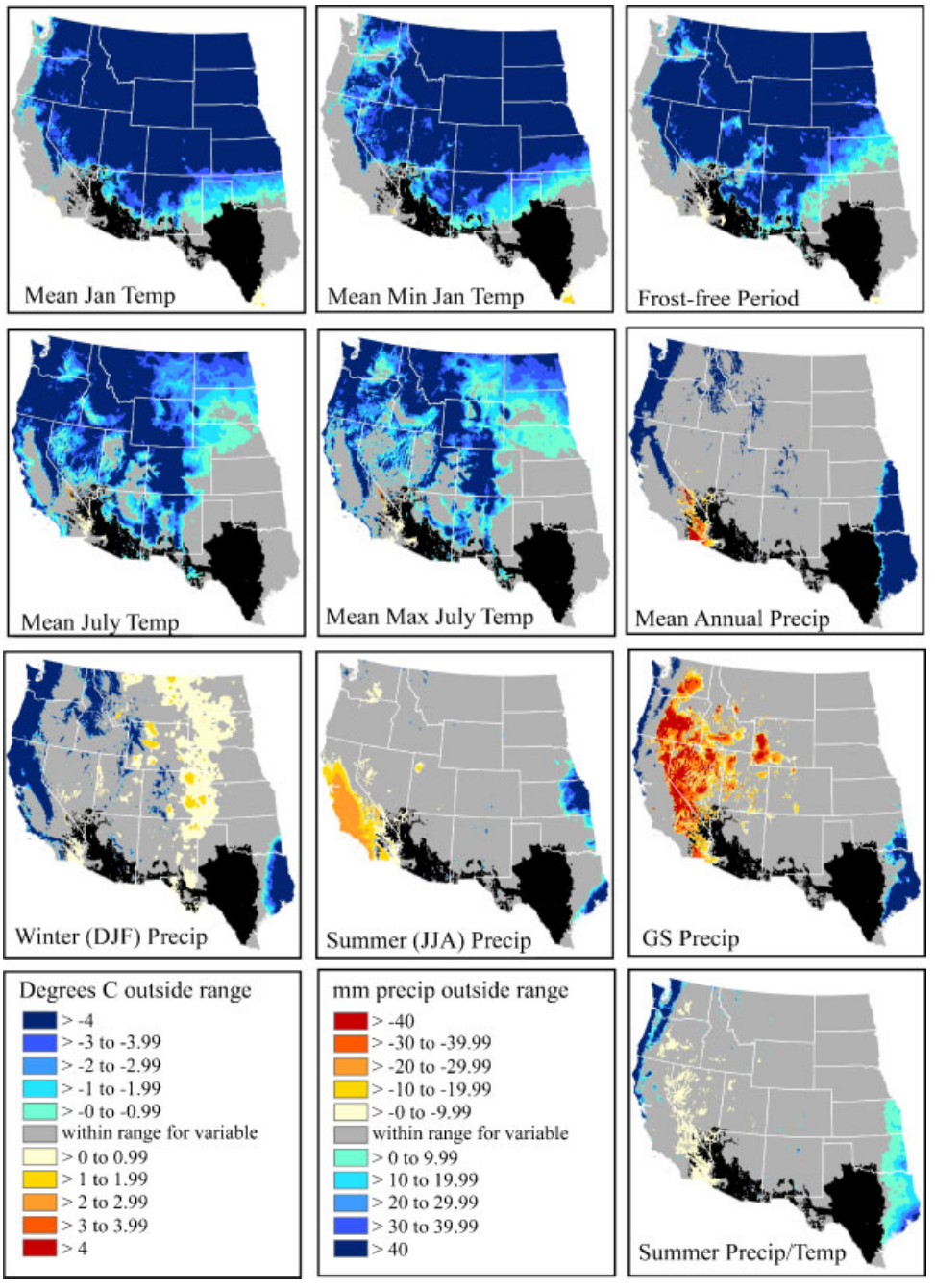

Figure 10 Niche space for C_3 *Acacia greggii*. This figure is available in colour online at www.interscience.wiley.com/journal/jqs

Mid- to late Holocene

A repeating theme across midden records (Fig. 1) is the early to mid-Holocene (13 000–5000 yr BP) absence and surprisingly late arrival (last 4000–5000 yr) of C_3 desert shrubs (including *Acacia constricta, Acacia greggii, Flourensia cernua, Fouquieria splendens* and *Larrea tridentata*) now common in the northern Chihuahuan Desert. During the mid-Holocene, conditions in the northern Chihuahuan Desert were marked by hot, moist summers and cold, dry winters. Expanded upper and lower treelines (Fall, 1997), northward expansion of C_4 grasses and tropical elements in packrat middens (Van Devender, 1990; McAuliffe and Van Devender, 1998), and climate model output (Rind, 1994; Kutzbach, 1998) all indicate greater-than-modern summer temperatures and precipitation during the mid-Holocene (ca. 8000–4000 yr BP). In contrast, desiccating or intermittent lakes from the USA–Mexico borderlands northward (Waters, 1989; Davis and Shafer, 1992; Anderson, 1993; Hasbargen, 1994; Krider, 1998), peak dune activity in the Great Plains (Forman *et al.*, 2001) and the decline in midden production throughout the southwestern United States (Webb and Betancourt, 1990; Spaulding, 1991) indicate pervasive mid-Holocene winter drought. While warm wet summers and dry winters would tend to favour C_4 grasses over C_3 desert shrubs, we suggest the absence of C_3 desert shrubs during the mid-Holocene was due to colder-than-present winter temperatures prior to ca. 5000–4000 yr BP noted in climate model simulations (Rind, 1994; Kutzbach, 1998).

Bioclimatic envelopes from desertscrub species clearly demonstrate the role of cold winter temperatures in defining the northern range limits for these species. This is consistent with evidence for reduced stature and vigour in *Fouquieria*

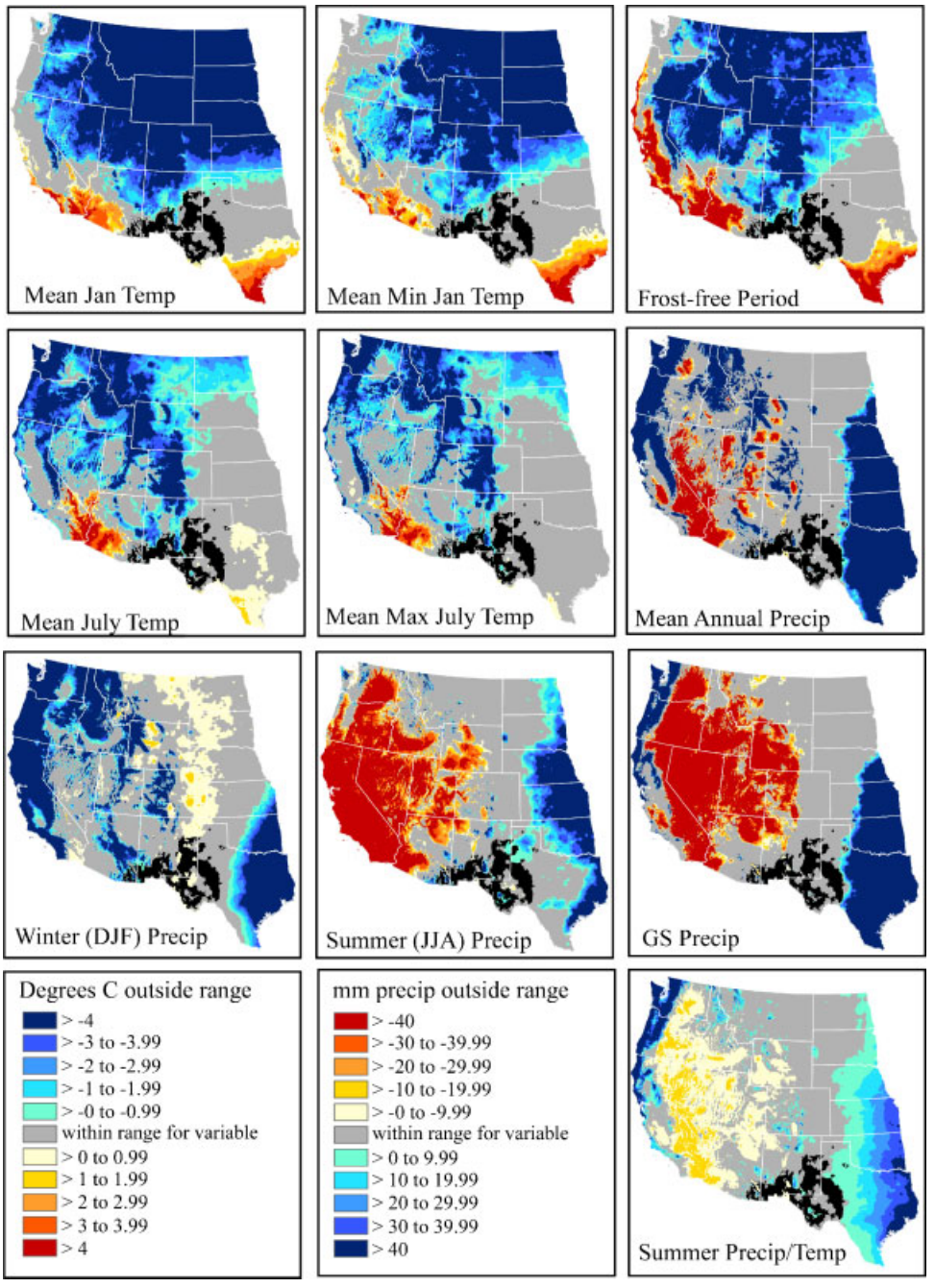

Figure 11 Niche space for C_3 *Flourensia cernua*. This figure is available in colour online at www.interscience.wiley.com/journal/jqs

splendens near its northern limit (Bradley, 1966), and freezing-induced xylem cavitation limiting the northern distribution of *Larrea tridentata* (Pockman and Sperry, 1997). Van Devender (1990) suggests that the northward advance of subtropical species was stymied by high frequencies of hard advective freezes due to incursions of Arctic air masses in the mid-Holocene (8000–4000), but accelerated when such freezes became less common in the late Holocene (4000–0 yr BP). Furthermore, desert shrubs may also have been limited by radiative freezes resulting from lower winter insolation during the early to mid-Holocene.

The arrival of desertscrub species in the northern Chihuahuan Desert around 5000–4000 yr BP corresponds to increasing winter insolation after reaching a minimum ca. 11 000 yr BP (Fig. 15), consistent with the advent of milder winter temperatures and a decrease in winter freezes. The northward expansion of desert shrub species appears to have occurred fairly quickly. For example, *Larrea tridentata* abruptly advanced to sites ranging from 1340–1430 to 1600–1985 m and was near its northernmost and uppermost limits at the Sevilleta Long Term Ecological Research (LTER) site by ca. 4100 yr BP. Exceptions are isolated, northern outposts, such as Isleta north of the Sevilleta LTER, where *Larrea* arrived more recently (after 300 yr BP) (Van Devender, 1990). After attaining their northern limits, subsequent northward progression for most desert shrubs appears to have been blocked by the higher topography and colder temperatures of the Colorado Plateau. We note that the northward migration of desert species tended to occur earlier in the Sonoran Desert (Van Devender, 1990; McAuliffe and Van Devender, 1998), which may have been due to pockets of warmer temperatures in the lower, hotter Sonoran Desert. There is also some evidence to indicate that

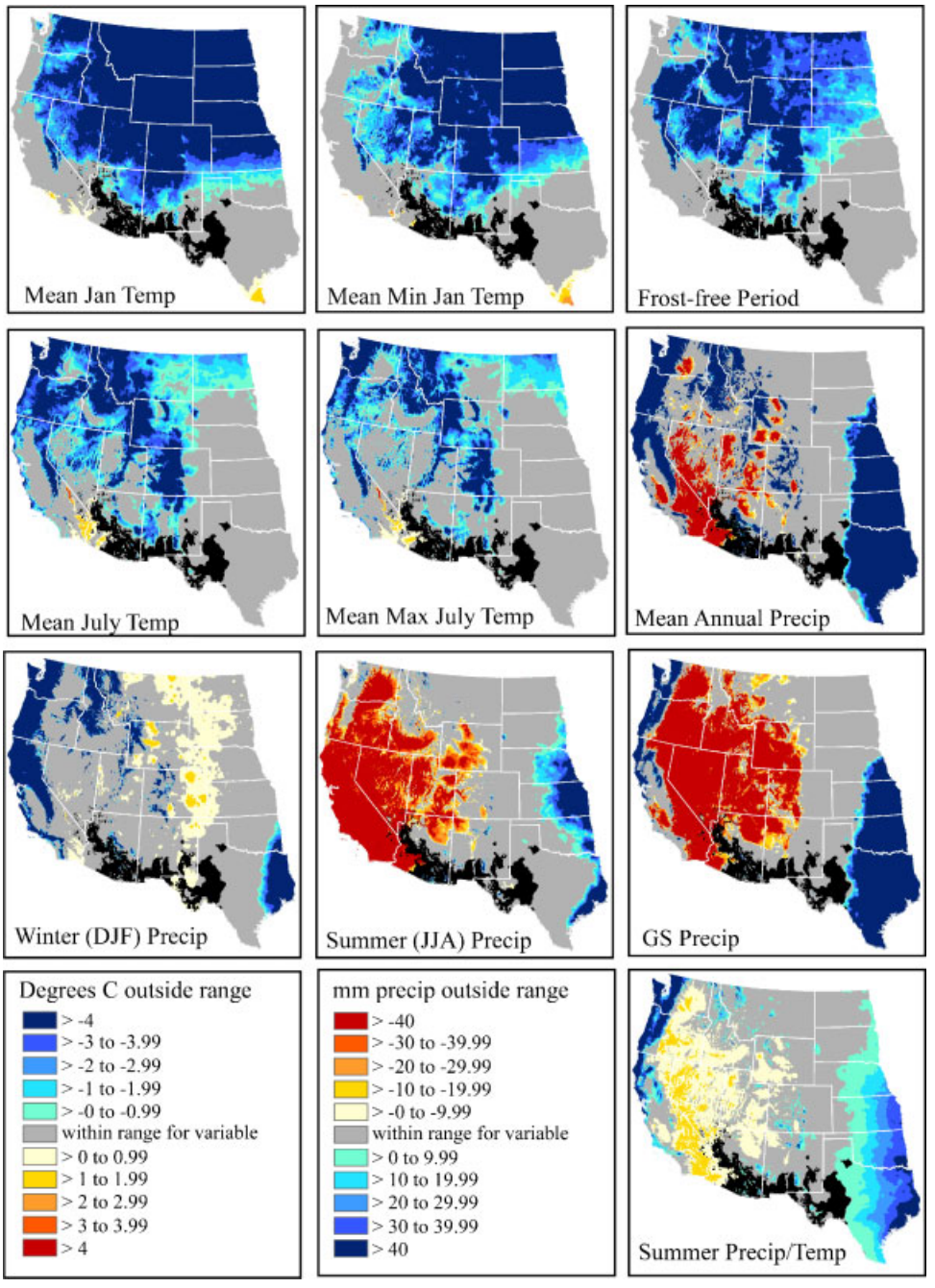

Figure 12 Niche space for C_3 *Fouquieria splendens*. This figure is available in colour online at www.interscience.wiley.com/journal/jqs

other subtropical shrubs are continuing to move into the northern Chihuahuan Desert, such as *Simmondsia chinensis* from the warmer Sonoran Desert to the west (Holmgren *et al.*, in press). Despite these exceptions, the transition to vegetation more modern in character around 5000–4000 yr BP in the northern Chihuahuan Desert appears to have been due, at least in part, to the ameliorisation of winter temperatures. The seemingly abrupt expansion of desert shrubs ca. 5000–4000 yr BP could mean that the climate forcing was equally abrupt or that some critical temperature threshold was crossed early on as winters warmed gradually.

Factors other than increasing winter temperatures also may have played a role in the modernisation of flora in the northern Chihuahuan Desert. For example, increased aridity and the resultant reduction in plant cover, leading to progressive erosion of the soil mantle and increased bare ground for colonisation, would tend to favour desertscrub species at the expense of grasses (Van Devender, 1995). Likewise, there is general consensus in proxy records and climate models that orbitally driven enhancement of the seasonal cycle during the mid-Holocene led to reduced ENSO variability prior to ca. 5000 yr BP and a more La-Niña-like average state, a condition correlated with drier winter conditions in the southwest (e.g. Rodbell *et al.*, 1999; Clement *et al.*, 2000). With the onset of greater ENSO frequency and magnitude in the later part of the mid-Holocene, the southwestern United States would have experienced more regular winter precipitation with greater extremes (Cane, 2005) and possibly higher freezing level heights, i.e. the elevation above sea level at which the air temperature is close to 0 °C (Diaz *et al.*, 2003). Increased ENSO strength beginning ca. 5000 yr BP, combined with warmer winter temperatures, may have favoured the

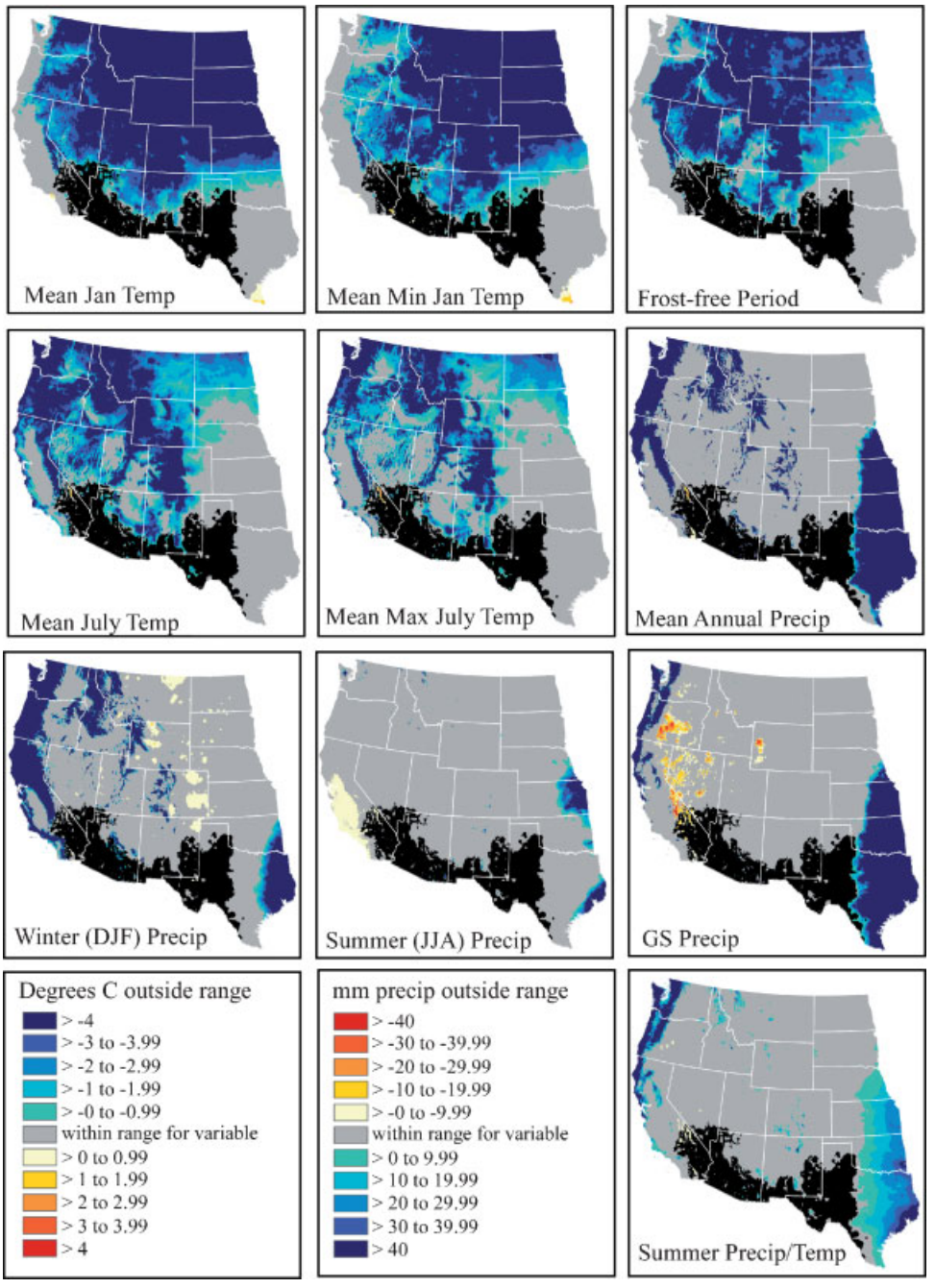

Figure 13 Niche space for C_3 *Larrea tridentata*

expansion of woody C_3 desert shrubs that respond to winter precipitation.

Finally, we acknowledge that the progressive 'modernisation' of vegetation in the northern Chihuahuan Desert may not be wholly in equilibrium with climate, but may be contingent on the exact sequence of climatic events and lagged ecological responses. The greater similarity of more recent fossil assemblages to present-day vegetation is likely to result, to some extent, from a shared history of climate variability, since the effects of drought-related mortality or greater recruitment during exceptionally wet years may leave a lasting imprint on the landscape (Swetnam and Betancourt, 1998). Likewise, landscape modification over time by species can lead to changes in plant community structure. For example, establishment of woody desert shrubs can alter microclimate and soil properties beneath their canopies where litter and nutrients accumulate, providing favourable microsites for some species while depleting resources in intercanopy areas. The resulting microsite heterogeneity between canopy and intercanopy areas may in turn affect the composition and spatial distribution of species (Charley and West, 1977; Vinton and Burke, 1995). The progressive modernisation of flora may have been due to such a feedback mechanism subsequent to mid-Holocene establishment of pioneer desert shrub species.

Conclusions

C_4-dominated desert grasslands represent one of the most stable biomes in North America. At their northern extent, these

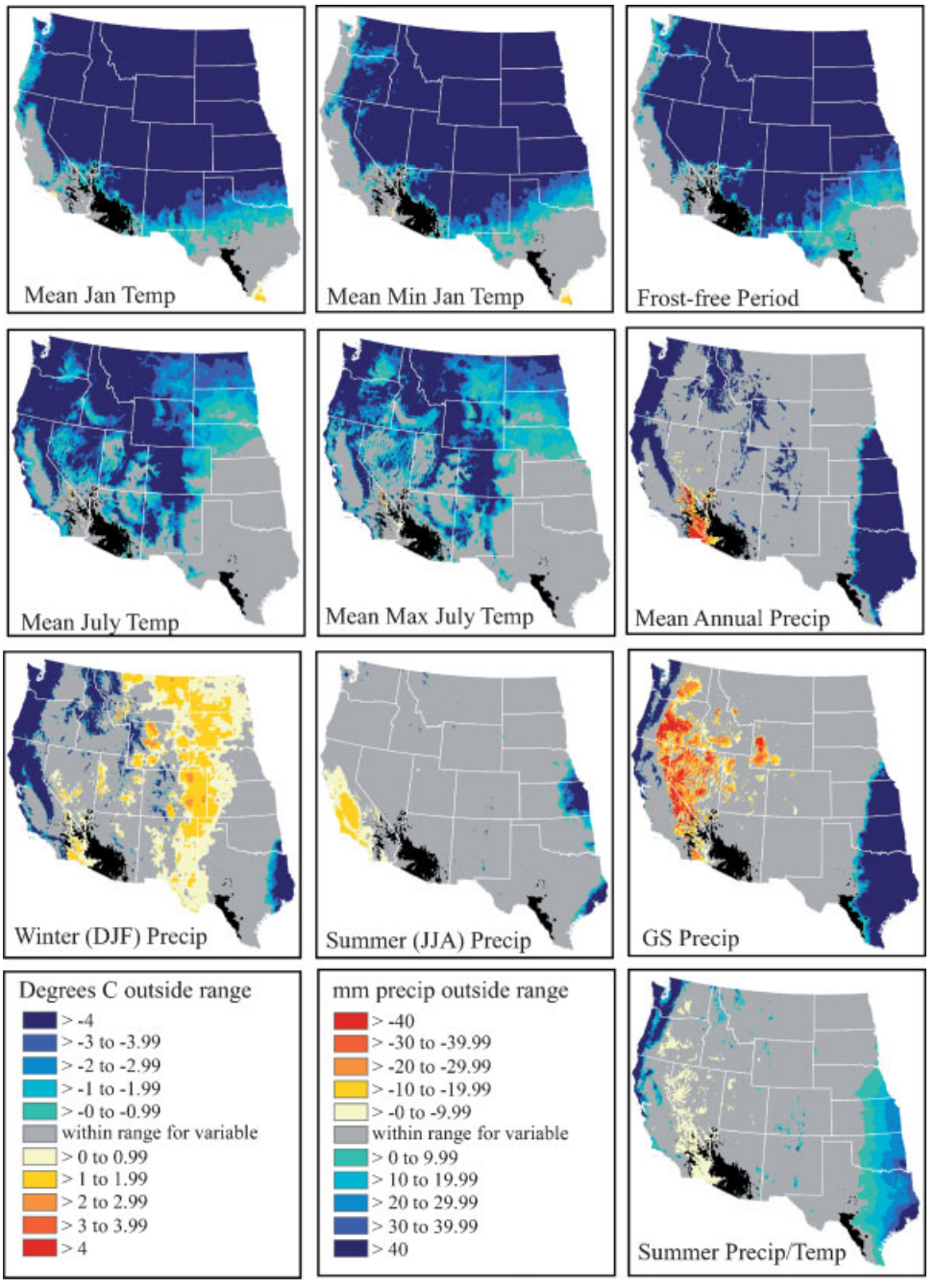

Figure 14 Niche space for C_3 *Simmondsia chinensis*

grasslands persisted in more or less the same geographic location through MIS 1, 2 and 3. This persistence is most easily explained by the glacial–interglacial permanence of warm winters and summer rainfall in the region. It should follow then that the core of the monsoon in the USA–Mexico borderlands and northern Chihuahuan Desert must have remained relatively intact throughout the last glacial–interglacial cycle. In its present form, the North American monsoon is primarily a Neogene phenomenon associated with formation of the Gulf of California (Lonsdale, 1989), which substituted cold, upwelling Pacific waters with the warm Sea of Cortez immediately west of the Sierra Madre Occidental.

The persistence of the core of the monsoon contrasts with conventional wisdom, mostly derived from coarsely resolved general circulation models, that southward displacement of the westerlies in glacial summers suppressed monsoonal circulation and rainfall over the southwestern USA (Kutzbach *et al.*, 1998; Thompson and Anderson, 2000). Mesoscale climate models have been able to resolve the present-day role of the Sea of Cortez and Sierra Madre Occidental in the multistage transport of moisture in the North American monsoon (Fawcett *et al.*, 2002). We submit that mesoscale models will eventually show a similar role during the Last Glacial Maximum and throughout the Quaternary. This permanence of summer rains and desert grassland, and the inconstancy of adjacent desert and woodland biomes, surely have left clear imprints on the biogeographic and evolutionary history of the region, akin to those outlined by Hafner and Riddle (2005).

Finally, the location of Pleistocene refugia for desert shrubs, presumably to the south in Mexico, remains elusive and warrants future study. Their abrupt arrival and expansion in the northern Chihuahuan Desert did not occur until ca.

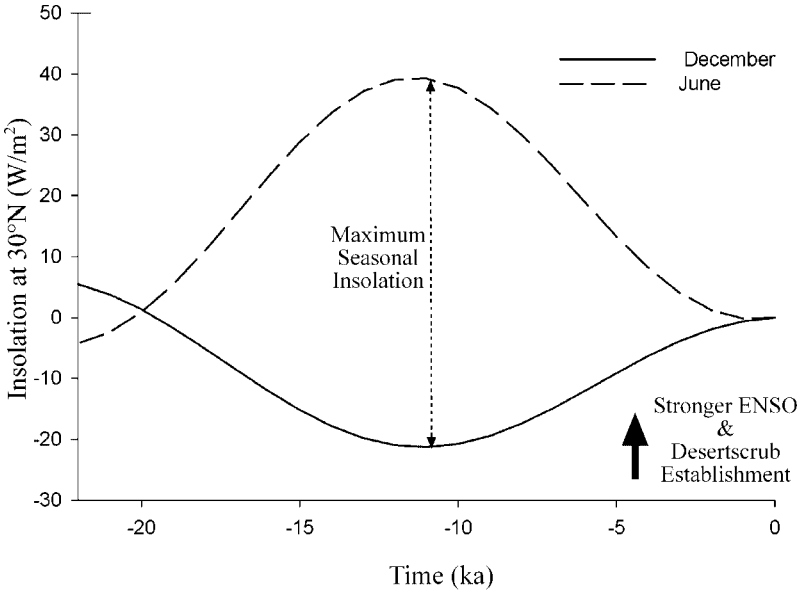

Figure 15 Changes in June and December insolation (W/m^2) relative to present for 30° N. Large arrow denotes step change in vegetation around 5000–4000 yr BP and onset of increased ENSO variability

5000–4000 yr BP, concurrent with increasing winter insolation and the onset of modern ENSO variability. It remains to be sorted out whether the warming that forced this expansion happened gradually or abruptly as a series of steps that may be ongoing.

Acknowledgements We thank J. Pelletier for providing computing resources and the following individuals for assistance obtaining herbarium records: K. Allred (NMCR), K. Birgy (UNLV), S. Boyd (RSA), B. Boyle (SALVIAS), Chris Frazier (UNM), R. Kaul (NEB), A. Kelsey (UT), C. Malone (RENO), R. Moe (JEPS, UC), C. Morse (KANU), A. Sanders (UCR), L. Schauer and R. Spellenberg (NMC), and D. Sutherland (OMA). We thank Sarah Metcalf for thoughtful comments.

References

Adams DK, Comrie, AC. 1997. The North American Monsoon. *Bulletin of the American Quaternary Research* **58**: 112–121.

Anderson RS. 1993. A 35,000 year vegetation and climate history from Potato Lake, Mogollon Rim, Arizona. *Quaternary Research* **40**: 351–359.

Arundel S. 2002. Modeling climate limits of plants found in Sonoran Desert packrat middens. *Quaternary Research* **58**: 112–121.

Atkinson TC, Briffa KR, Coope GR, Joachim MJ, Perry DW. 1986. Climatic calibration of coleopteran data. In *Handbook of Holocene Palaeoecology and Palaeohydrology*, Berglund BE (ed.). Wiley-Interscience: Chichester, UK; 851–858.

Betancourt JL. 1984. Late Quaternary plant zonation and climate in southeastern Utah. *Great Basin Naturalist* **44**: 1–35.

Betancourt JL. 1990. Late Quaternary biogeography of the Colorado Plateau. In *Packrat Middens—The Last 40,000 Years of Biotic Change*, Betancourt JL, Van Devender TR, Martin, PS (eds). University of Arizona Press: Tucson, AZ; 259–292.

Betancourt JL. 2004. Arid lands paleobiogeography: the rodent midden record in the Americas. In *Frontiers in Biogeography*, Lomolino MV, Heaney, LR (eds). Sinauer Associates, Inc.: Sunderland, MA; 27–46.

Betancourt JL, Rylander KA, Peñalba C, McVickar JL. 2001. Late Quaternary vegetation history of Rough Canyon, south-central New Mexico, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* **165**: 71–95.

Bradley WG. 1966. Populations of two Sonoran Desert plants, and deductions as to factors limiting their northward extension. *Southwestern Naturalist* **11**: 395–401.

Brewer S, Cheddadi R, de Beaulieu JL, Reille M. 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. *Forest Ecology and Management* **156**: 27–48.

Brown JH, Lomolino MV. 1998. *Biogeography*. Sinauer Associates, Inc.: Sunderland, MA.

Cane MA. 2005. The evolution of El Niño, past and future. *Earth and Planetary Science Letters* **230**: 227–240.

Charley JL, West NE. 1977. Micro-patterns of nitrogen mineralization activity in soils of some shrub-dominated semi-desert ecosystems of Utah. *Soil Biology and Biochemistry* **9**: 357–365.

Clement AC, Seager R, Cane MA. 2000. Suppression of El Niño during the mid-Holocene by changes in the Earth's orbit. *Paleoceanography* **15**: 731–737.

Connin SL, Betancourt JL, Quade J. 1998. Late Pleistocene C_4 plant dominance and summer rainfall in the southwestern United States from isotopic study of herbivore teeth. *Quaternary Research* **50**: 197–193.

Daly C, Taylor GH, Gibson WP. 1997. The PRISM approach to mapping precipitation and temperature. In *Proceedings of the 10th American Meteorological Society Conference,* American Meteorological Society: Boston, MA; 10–12.

Davis OK, Shafer WD. 1992. A Holocene climatic record for the Sonoran Desert from pollen analysis of Montezuma Well, Arizona, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* **92**: 107–119.

Diaz HF, Eischeid JK, Duncan C, Bradley RS. 2003. Variability of freezing levels, melting season indicators, and snow cover for selected high-elevation and continental regions in the last 50 years. *Climatic Change* **59**: 33–52.

Ehleringer JR, Cerling TE, Helliker BR. 1997. C_4 photosynthesis, atmospheric CO_2, and climate. *Oecologia* **112**: 285–299.

Elias SA. 1997. The mutual climatic range method of palaeoclimate reconstruction based on insect fossils: new applications and interhemispheric comparisons. *Quaternary Science Reviews* **16**: 1217–1225.

Fall PL. 1997. Timberline fluctuations and late Quaternary paleoclimates in the Southern Rocky Mountains, Colorado. *GSA Bulletin* **109**: 1306–1320.

Fawcett PJ, Stalker JR, Gutzler DS. 2002. Multistage moisture transport into the interior of northern Mexico during the North American summer monsoon. *Geophysical Research Letters* **29**: 1–4.

Fleischhauer HL, Stone WJ. 1982. *Quaternary geology of Lake Animas, Hidalgo County, New Mexico. New Mexico Bureau of Mines and Mineral Resources Circular* 174, Socorro, New Mexico.

Forman SL, Oglesby R, Webb RS. 2001. Temporal and spatial patterns of Holocene dune activity on the Great Plains of North America: megadroughts and climate links. *Global and Planetary Change* **29**: 1–29.

Hafner DJ, Riddle BR. 2005. Mammalian phylogeography and evolutionary history of northern Mexico's deserts. In *Biodiversity, Ecosystems, and Conservation in Northern Mexico*, Ceballos G, Catron J-L (eds). Oxford University Press: Oxford.

Hasbargen J. 1994. A Holocene paleoclimatic and environmental record from Stoneman Lake, Arizona. *Quaternary Research* **42**: 188–196.

Hawley JW, Hibbs HJ, Kennedy JF, Creel BJ, Remmenga MD, Johnson M, Lee M., Dinterman P. 2000. *Trans-international boundary aquifers in southwestern New Mexico*. New Mexico Water Resources Research Institute, Technical Completion Report, Interagency Contract No. X-996-350-01-3 (http://wrri.nmsu.edu/publish/otherrpt/swnm/).

Holmgren CA, Betancourt JL, Rylander KA. In press. A 36 200-yr vegetation history from the Peloncillo Mountains, southwestern Arizona, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Holmgren CA, Peñalba MC, Rylander KA, Betancourt JL. 2003. A 16,000 ^{14}C yr B.P. packrat midden series from the USA–Mexico Borderlands. *Quaternary Research* **60**: 319–329.

Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology* **22**: 415–427.

Jackson ST, Overpeck JT. 2000. Responses of plant populations and communities to long-term environmental changes of the late Quaternary. In *Deep Time: Paleobiology's Perspective*, Erwin DH, Wing SL (eds). Supplement to *Paleobiology* **26**: 194–220.

Koch PL, Diffenbaugh NS, Hoppe KA. 2004. The effects of late Quaternary climate and pCO_2 change on C_4 plant abundance in the south-central United States. *Palaeogeography, Palaeoclimatology, Palaeoecology* **207**: 331–357.

Krider PR. 1998. Paleoclimatic significance of late Quaternary lacustrine and alluvial stratigraphy, Animas Valley, New Mexico. *Quaternary Research* **50**: 283–289.

Kubien DS, von Caemmerer S, Furbank RT, Sage RT. 2003. C_4 photosynthesis at low temperature. A study using transgenic plants with reduced amounts of Rubisco. *Plant Physiology* **132**: 1577–1585.

Kutzbach J, Gallimore R, Harrison S, Behling P, Selin R, Laarif F. 1998. Climate and biome simulations for the past 21,000 years. *Quaternary Science Reviews* **17**: 473–506.

Liu B, Phillips FM, Campbell AR. 1996. Stable carbon and oxygen isotopes of pedogenic carbonates, Ajo Mountains, southern Arizona: implications for paleoenvironmental change. *Palaeogeography, Palaeoclimatology, Palaeoecology* **124**: 233–246.

Long A. 1966. *Late Pleistocene and Recent chronologies of Playa Lakes in Arizona and New Mexico*. PhD dissertation, University of Arizona, Tucson.

Long SP. 1983. C_4 photosynthesis at low temperatures. *Plant, Cell and Environment* **6**: 345–363.

Long SP. 1999. Environmental responses. In *The Biology of C_4 photosynthesis*, Sage RF, Monson RK (eds). Academic Press: San Diego, CA; 215–249.

Lonsdale P. 1989. Geology and tectonic history of the Gulf of California. In *The Eastern Pacific Ocean and Hawaii*, Winterer EL, Hussong DM, Decker RW (eds). The Geological Society of America: Boulder, Vol. N; 499–521.

McAuliffe JR, Van Devender TR. 1998. A 22,000-year record of vegetation change in the north-central Sonoran Desert. *Palaeogeography, Palaeoclimatology, Palaeoecology* **141**: 253–375.

Monger HC, Cole DR, Gish JW, Giordano TH. 1998. Stable carbon and oxygen isotopes in Quaternary soil carbonates as indicators of ecogeomorphic changes in the northern Chihuahuan Desert, USA. *Geoderma* **82**: 137–172.

Norris J, Jackson ST, Betancourt JL. 2006. A classification tree analysis of the distribution of ponderosa pine in the western U.S.A. *Journal of Biogeography* **33**: 342–360.

Pearson RG, Dawson TP, Berry PM, Harrison PA. 2002. SPECIES: a spatial evaluation of climate impact on the envelope of species. *Ecological Modelling* **154**: 289–300.

Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? *Global Ecology and Biogeography* **12**: 361–371.

Pockman WT, Sperry JS. 1997. Freezing-induced cavitation and the northern limit of *Larrea tridentata*. Oecologia **109**: 19–27.

Potvin C, Simon J-P, Strain BR. 1986. Effect of low temperature on the photosynthetic metabolism of the C_4 grass *Echinochloa crus-galli*. *Oecologia* **69**: 499–506.

Rind D. 1994, General Circulation Model Output Data Set. IGBP PAGES/World Data Center for Paleoclimatology Data Contribution Series # 94-012. NOAA/NGDC Paleoclimatology Program, Boulder, CO, USA.

Rodbell DT, Seltzer GO, Anderson DM, Abbott MB, Enfield DB, Newman JH. 1999. An ~15,000-year record of El Niño-driven alluviation in southwestern Ecuador. *Science* 283: 516–520.

Sage RF, Sage TL. 2002. Microsite characteristics of *Muhlenbergia richardsonis* (Trin.) Rydb., an alpine C_4 grass from the White Mountains, California. *Oecologia* **132**: 501–508.

Schmitz TJ, Mullen SL. 1996. Water vapor transport associated with the summertime North American monsoon as depicted by ECMWF analyses. *Journal of Climate* **9**: 1621–1633.

Schwarz AG, Reaney, JT. 1989. Perenniating structures and freezing tolerance of northern and southern populations of C_4 grasses. *Botanical Gazette* **150**: 239–246.

Sharpe SE. 2002. Constructing seasonal climograph overlap envelopes from Holocene packrat midden contents, Dinosaur National Monument, Colorado. *Quaternary Research* **57**: 306–313.

Spaulding WG. 1991. A middle Holocene vegetation record from the Mojave Desert of North America and its paleoclimatic significance. *Quaternary Research* **35**: 427–437.

Stensrud DJ, Gall R, Mullen S, Howard K. 1995. Model climatology of the Mexican Monsoon. *Monthly Weather Review* **125**: 417–437.

Stockwell DRB, Noble IR. 1991. Induction of sets of rules from animal distribution data: a robust and informative method of data analysis. *Mathematics and Computers in Simulation* **32**: 49–254.

Swetnam TW, Betancourt JL. 1998. Mesoscale disturbance and ecological response to decadal-scale climate variability in the American Southwest. *Journal of Climate* **11**: 3128–3147.

Teeri JA, Stowe LG. 1976. Climatic patterns and the distribution of C_4 grasses in North America. *Oecologia* **23**: 1–12.

Thompson RS, Anderson KH. 2000. Biomes of western North America at 18,000, 6000 and 0 ^{14}C yr BP reconstructed from pollen and packrat midden data. *Journal of Biogeography* **27**: 555–584.

Thompson RS, Whitlock C, Bartlein PJ, Harrison SP, Spaulding WG. 1993. Climatic changes in the western United States since 18,000 yr BP. In *Global Climates since the Last Glacial Maximum*, Wright HE (ed.). University of Minnesota Press: St Paul, MN; 468–513.

Thompson RS, Anderson KH, Bartlein PJ. 1999. *Quantitative paleoclimatic reconstructions form late Pleistocene macrofossils of the Yucca Mountain region*. USGS Open-File Report 99–338.

Turner RM, Bowers JE, Burgess TL. 1995. *Sonoran Desert Plants: An Ecological Atlas*. The University of Arizona Press: Tucson, AZ.

Van Devender TR. 1987. Holocene vegetation and climate in the Puerto Blanco Mountains, southwestern Arizona. *Quaternary Research* **27**: 51–72.

Van Devender TR. 1990. Late Quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. In *Packrat Middens—The Last 40,000 Years of Biotic Change*. Betancourt JL, Van Devender TR, Martin, PS (eds). University of Arizona Press: Tucson, AZ; 104–133.

Van Devender TR. 1995. Desert grassland history. In *The Desert Grassland: Changing Climates, Evolution, Biogeography, and Community Dynamics*, McClaran MP, Van Devender TR (eds). University of Arizona Press: Tucson, AZ; 65–99.

Van Devender TR, Burgess TL. 1985. Late Pleistocene woodlands in the Bolson de Mapimi: a refugium for the Chihuahuan Desert biota? *Quaternary Research* **24**: 346–353.

Van Devender TR, Riskind DH. 1979. Late Pleistocene and early Holocene plant remains from Hueco Tanks State Historical Park: the development of a refugium. *Southwestern Naturalist* **24**: 147–140.

Van Devender TR, Toolin LJ. 1983. Late Quaternary vegetation of the San Andres Mountains, Sierra County, New Mexico. In *The Prehistory of Rhodes Canyon: Survey and Mitigation*, Eidenbach PL (ed.).

Report to Holloman Air Force Base, Human Systems Research, Inc.: Tularosa, NM; 33–54.

Van Devender TR, Betancourt JL, Wimberley M. 1984. Biogeographic implications of a packrat midden sequence from the Sacramento Mountains, south-central New Mexico. *Quaternary Research* **22**: 344–360.

Van Devender TR, Thompson RS, Betancourt JL. 1987. Vegetation history of the deserts of southwestern North America: the nature and timing of the Late Wisconsin–Holocene transition. In *North America and Adjacent Oceans during the Last Deglaciation. The Geology of North America.* Ruddiman WF, Wright HE (eds). Geological Society of America: Boulder, CO; 323–352.

Vinton MA, Burke IC. 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology* **76**: 1116–1133.

Waters MR. 1989. Late Quaternary lacustrine history and paleoclimatic significance of pluvial Lake Cochise, southeastern Arizona. *Quaternary Research* **32**: 1–11.

Webb RH, Betancourt JL. 1990. The spatial and temporal distribution of radiocarbon ages from packrat middens. In *Packrat Middens—The Last 40,000 Years of Biotic Change*, Betancourt JL, Van Devender TR, Martin PS (eds). University of Arizona Press: Tucson, AZ; 85–102.

Whiteman CD, Ban X, Sutherland JL. 1999. Wintertime surface wind patterns in the Colorado River Valley. *Journal of Applied Meteorology* **38**: 1118–1130.

Williams JW, Shuman BN, Webb T. 2001. Dissimilarity analyses of late-Quaternary vegetation and climate in eastern North America. *Ecology* **82**: 3346–3362.

Woodward FI. 1987. *Climate and Plant Distribution.* Cambridge University Press: Cambridge, MA.