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A long-term perspective on woody plant encroachment in the desert southwest, New Mexico, USA

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Keywords

Charcoal; Fire; Grazing; Madrean woodland; Paleoecology; Pollen

Abbreviations

cal yr BP = calibrated years before present; CHAR = charcoal accumulation rate; ENSO = El Niño/Southern Oscillation; PDSI = palmer drought severity index

Nomenclature

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Abstract

Objective: To assess potential causes of woody plant encroachment into desert grassland systems using a 5500-yr-old sediment record from a ciénega in New Mexico.

Location: Cloverdale Ciénega, southwestern New Mexico.

Methods: Utilizing fossil pollen and charcoal preserved in wetland sediments, a long-term record of variations in vegetation composition and fire activity was generated. The record was compared to published data on drought, the El Niño/Southern Oscillation (ENSO), carbon dioxide concentrations and known dates of grazing impacts to evaluate various hypotheses regarding the timing and causes of woody plant encroachment in desert grasslands.

Results: The woody plant encroachment observed in the past 200 yrs is unprecedented in the context of the previous 5500 yrs of vegetation history. The observed increase in woody plant abundance was not related to droughts or changes in ENSO event frequency, and was contemporaneous with the rise in atmospheric CO_2 and known grazing impacts. Charcoal influx increased in conjunction with historic woody plant pollen abundance and therefore the encroachment was not related to fire exclusion.

Conclusions: The long-term sediment record from Cloverdale Ciénega provides the context for evaluation of the various hypotheses for woody plant encroachment. At Cloverdale Ciénega we demonstrate that woody plant encroachment of the last 200 yrs is unprecedented and outside of the historic natural range of variability of the previous five millennia. We also demonstrate that woody plant encroachment is not related to climatological changes such as drought or increases in ENSO frequency. Increases in woody plant pollen are associated with increases in carbon dioxide, and high-intensity grazing during the late 19th and early 20th centuries.

Introduction

Historic encroachment of woody plants into grassland or savanna ecosystems is observed worldwide, and the causes and mechanisms are still being discussed and debated (see Archer et al. 2001, Table 1; Morgan et al. 2007; Van Auken 2009; Bowman et al. 2010; Bond & Midgley 2012). Woody plant encroachment into grassland ecosystems of the US desert southwest (hereinafter ‘Southwest’) has been discussed in the literature since as early as the 1930s, particularly in terms of maintaining open ranges for grazers such as cattle and reducing competition among grasses, shrubs, cacti and tree taxa (e.g. Dameron 1939; Bell & Dyksterhuis 1943; Parker & Martin 1952). Woodland encroachment into grassland settings is a concern because it not only changes natural rangeland habitat, but is thought to affect water availability and grazing resources. Numerous hypotheses have been proposed to explain Madrean woodland expansion across the semi-arid grasslands. However, the earliest records of vegetation composition from the Southwest are associated with Euro-American settlement and exploration. These records are biased by activities of resource exploitation, and were often conducted after human activity had already changed the landscape (Mearns 1907; Hastings 1959; Buffington & Herbel 1965; Davis et al. 1982, 2002). *Post-hoc* observations

Table 1. Dates utilized in the Cloverdale Ciénega age model.

Depth	Core	Lab Number	Method	Material	^{14}C age	Error	Calibrated (CALIB 6.0) cal yr BP 2 Sigma
0–1	CC08C		Surface				−58
14–15	CC08C		Lead-210			1	89
47–48	CC08C	4477	AMS	Pollen	2370	45	2322–2504
63–64	CC08C	5469	AMS	Pollen	2770	25	2789–2928
95–96	CC08C	5470	AMS	Pollen	3280	30	3443–3579
159–160	CC08C	4478	AMS	Pollen	4530	45	5040–5318

have only served to provide a biased record with which to evaluate the timing and potential causes of woody plant encroachment into the grasslands of the Southwest.

Semi-arid grasslands of the Southwest, while extensive, are discontinuous and usually occur between elevations of 1100–2500 m (McClaran 1995; Van Auken 2000). In the Southwest, semi-arid grasslands are difficult systems to classify as they contain many different vegetation components, including shrubs and trees (Burgess 1995; McClaran 1995) and inter-finger with Sonoran Desert shrublands at lower elevations and evergreen oak woodlands at higher elevations (Van Auken 2000). There are distinctive features used to classify desert grasslands that allow the determination of whether woody encroachment has occurred (Burgess 1995), but the main criteria is the *dominance* of woody taxa over grass taxa.

Woody or ‘problem’ taxa *Larrea tridentata* (creosote) and *Prosopis* spp. (mesquite) have been identified as the most significant encroachers, but other problem taxa include *Acacia, Yucca, Opuntia* (prickly pear), *Gutierrezia* (snakeweed), *Juniperus* (juniper) and *Quercus* (oak) (Van Auken 2000). The causes of the encroachment have been hypothesized as driven by increases in atmospheric CO_2, climate change, land use (specifically grazing) or fire exclusion (Grover & Musick 1990; Idso 1992; Polley et al. 1997; Van Auken 2000, 2009; Morgan et al. 2007; Bond & Midgley 2012). Of these, intensive cattle grazing has been most cited as the primary factor in the conversion of semi-arid grasslands into shrublands or woodlands, with climate change as a confounding factor (Grover & Musick 1990; Bahre 1995; Van Auken 2000, 2009; Bond & Midgley 2012), although the impact of increased atmospheric CO_2 has received more attention in recent literature (Polley et al. 1997; Morgan et al. 2007; Bond & Midgley 2012). The problem in assessing competing hypotheses as the mechanisms for grassland conversion is that there have not been appropriate independent data sets available for evaluating competing hypotheses that exceed the 150 yrs of observational records.

To provide an assessment of the natural range of variability of woodland encroachment into grasslands based on pre-European community structure, fire activity and climate, we utilize paleoenvironmental data from a wetland near the upper elevation transition of grassland to woodlands in southwestern New Mexico. The paleoenvironmental record from Cloverdale Ciénega spans the last ~5500 yrs. This record, in association with long-term records of climate and CO_2 concentrations, allows us to assess the multiple hypotheses related to the timing and causes of the conversion of desert grassland to Madrean woodland. The competing hypotheses for woody encroachment include:

H_0: Natural variation – woody plant abundance increases and decreases over time as part of the natural range of variability.
H_1: Climate change.
$H_{1.1}$ Drought – changes in effective moisture force changes in composition from grass to woody plant-dominated ecosystems.
$H_{1.2}$ El Niño/Southern Oscillation (ENSO) – Ocean–atmosphere interactions result in fluctuations in seasonal precipitation patterns responsible for woody plant encroachment.
H_2: Changes in CO_2 concentrations – increases in CO_2 concentrations in the atmosphere favour woody plant growth, as indicated by CO_2 fertilization experiments.
H_3: Changes in fire regime – post Euro-American settlement fire suppression allowed the establishment of more woody plants within grassland environments.
H_4: Grazing – intensive grazing in the late 1800s promoted a shift to increased woody plants due to high levels of grass herbivory and compaction of soils.

Site description

Cloverdale Ciénega is located in the Peloncillo Mountains, Coronado National Forest, NM (31°26.141′ N, 108°58.517 W, 1640 m a.s.l.; Fig. 1). Cloverdale Ciénega is situated at the ecotone between Madrean woodland and grassland (Marshall et al. 2006), making this location potentially sensitive to changes in community composition over time. Currently, the Madrean woodlands form a mosaic of clustered tree stands interspersed with patches of shrub and grass (Brown 1982).

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Fig. 1. Location map for Cloverdale Ciénega.

Plant community types

Madrean evergreen woodland

This mild winter/wet summer woodland is centred in the Sierra Madre Occidental of Mexico, reaching northward to the mountains of southern Arizona, southwestern New Mexico and Trans-Pecos Texas. At its lower elevations, the woodland is typically open to very open. Trees are evergreen oaks (*Quercus* spp.) from 6 to >15 m in height, alligator bark (*Juniperus deppeana*) and one-seed (*Juniperus monosperma*) junipers, and Mexican pinyon pine (*Pinus cembroides*) in unequal proportions (known as 'encinal'). In the inter-mountain regions of sub-Mogollon Arizona and the Chiricahua Mountains, the oaks most prevalent in the encinal are *Q. emoryi* (Emory oak), and *Q. arizonica* (Arizona white oak; Brown 1982).

On the eastern slopes of the Sierra Madre Occidental in west Texas, New Mexico and isolated mountain ranges in southeastern Arizona, the lower contact with Madrean evergreen woodland is grassland. This contact is apparently determined to a large extent by soil depth and type. Since woodlands occupy much the same elevation range as grasslands, the lower encinal communities here are at ca. 1500–1800 m a.s.l., along drainages, on rocky slopes and other thin-soiled habitats (Brown 1982).

Woodlands around Cloverdale Ciénega contain woody shrub species such as *Rhus aromatica* (sumac), *Rosa woodsii* (rose) and *Garrya wrightii* (coffeeberry) in the small canyon above the wetland. Most of the understorey grasses are *Schizachryrium scoparium* (little bluestem) and *Bouteloua curtipendula* (sideoats grama).

In the upland areas near Cloverdale Ciénega the landscape is similar to true grassland. Here, dominant upland grassland species include *Bouteloua* spp. (blue and black grama), *Hilaria mutica* (tobosa) and *Sporobolus wrightii* (big alkalai sacaton). Some non-native grasses are present, such as *Bromus inermis* (bromegrass) and *Agrostis gigantea* (bentgrass).

Riparian

Riparian corridor species in the region include *Fraxinus velutina* (Arizona ash), *Juglans major* (walnut), *Salix bonpladiana, S. exigua* (willows), and in some areas *Platanus wrightii* (Arizona sycamore). On more xeric and/or degraded areas *Prosopis velutina* and *Prosopis glandulosa* (mesquite) are present.

Within the riparian corridors lie desert wetlands, or ciénegas, in reaches that are broad and considered largely aggradational (Hendrickson & Minckley 1985; Minckley & Brunelle 2007; Minckley et al. 2013). Most plants restricted to these perennially wet areas are monocotyledon species such as aquatic or semi-aquatic sedges like *Eleocharis* spp., *Cyperus* spp. and *Juncus* spp.,but also includes *Callitriche heterophylla* (water starwort), *Lemna* sp. (duckweed), *Limosella aquatica* (mudwort), *Ludwigia palustris* (water purslane), *Alisma triviale* (water plantain) and *Sagittaria longiloba* (longbarb arrowhead).

Methods

Field

Collection of flowering plants from the ciénega and surrounding uplands was conducted using volunteers of the Sky Island Alliance, Tucson, AZ. Secondary sampling was conducted during the collection of sediment cores to identify major tree and shrub taxa and augment taxa that might have been overlooked by the volunteer efforts.

Sediment cores were collected using a vibracore system (Vibracore Technologies, Long Lake, NY, US) where manual probes indicated maximum sediment accumulation. The vibracore apparatus uses a cement levelling motor attached to a 3-inch aluminium tube inserted into the sediments until refusal (bedrock). Sediment was retained in the aluminium tube by placing an airtight cap on the top of the tube to create a vacuum, allowing the sediment core to be removed from the ground without loss. The core was transported in the aluminium tube to the University of Utah and split in the lab for description and sampling.

Laboratory

Once the core was removed from the aluminium tube, the colour and texture of the sediments were described (Appendix S1). Every contiguous centimeter of the core was examined for charcoal analysis. For pollen analysis, samples were collected temporally to acquire high-resolution data for the last 250 yrs (range 4–96 yrs between samples, mean 40 yrs), and samples of approximately every 200 yrs for the remainder of the core.

Age–depth relationships were determined for the sediments based on four AMS (accelerator mass spectrometry) dates on pollen concentrates, a lead-210 chronology and the surface collection year (2008 CE: −58 yrs cal yr BP) date (Table 1). Ages are presented in calibrated years before present (cal yr BP) where 1950 CE is equal to yr 0 cal yr BP. The age–depth model was generated in CLAM (Blaauw 2010) using a smoothing spline for the entire record (0.10 smoother; goodness of fit = 22.4). The extrapolated basal age of the record was 5342 cal yr B.P (Fig. S1). The resulting age–depth relationships are consistent with other well-dated ciénega deposits around the Southwest (A. Brunelle, unpublished data; Minckley & Brunelle 2007).

Pollen extraction methods followed Faegri et al. (1989). At least 300 terrestrial pollen grains or *Lycopodium* (exotic spore added as a tracer) were tallied for each depth. Pollen grains were identified at a magnification of 500× to the lowest possible taxonomic classification using published atlases (e.g. Erdtman 1969; Kapp et al. 2007). Counts were converted to percentages based on the sum of total terrestrial grains, and influx determined by using the sedimentation rate, which was calculated using the age model (Fig. S2). Influx data provide a better indicator of changes in specific taxa as they are independent measures of the abundance of a given taxon, unlike percentage data, which are dependent on the changes in abundance of the rest of the pollen assemblage. Pollen influx data can be used to extract signals in the pollen data that might be lost in a traditional percentage diagram (Mehringer et al. 1977). Influx data are also better suited for interpreting changes in vegetation composition in ecotone environments, where small changes in pollen abundance can represent significant changes in landscape composition (Hicks & Hyvärinen 1999). Encroacher (woody species) influx was calculated by summing the influx values for *Larrea*, *Prosopis*, *Quercus*, *Agave* and *Yucca*. These taxa, all of which were present in the fossil assemblage, are commonly described as encroachers in related literature (Van Auken 2000).

Charcoal analysis for fire history is based on 5-cm^3 volumetric samples using standard methods and rationale (Conedera et al. 2009). Taphonomic studies of large particle deposition on fluvial wetland surfaces and isotopic analysis of ciénega sediments suggests sedimentation of charcoal fragments would be similar to those of lake and bog surfaces (Traverse 1994; Minckley et al. 2009). Charcoal concentrations (particles cm^{-3}) were converted to influx (particles cm^{-2}·yr^{-1}) using the age model.

The EPICA Dome C Ice Core High Resolution Holocene and Transition CO_2 data (Monnin et al. 2004) and the Siple Station Historic CO_2 data (Neftel et al. 1994) were used for records of atmospheric CO_2. The Siple Station data only cover to 1953 CE, so Mauna Loa yearly average data were used from the onset of collection (1959 CE) to 2012 CE (Tans & Keeling, accessed 2013).

The Palmer drought severity index (PDSI) reconstructions based on tree ring data for North America (Cook et al. 2004) were used for records of drought.

Grazing intensity data for major ranching activity (cattle and sheep) are not available as a time series, so we use estimations of grazing intensity from previously published works (Culbert 1941; Bahre 1995). However, these data are geographically generalized and not necessarily reflective of grazing intensity near Cloverdale Ciénega.

Results

The data, presented here in two formats, are primary data collected from Cloverdale Ciénega sediments (pollen and charcoal). Figure 2 represents the entirety of the Cloverdale Ciénega record (~5500 yrs), while Fig. 3 focuses on the last 1000 yrs to highlight the changes associated with the encroachment of woody plants.

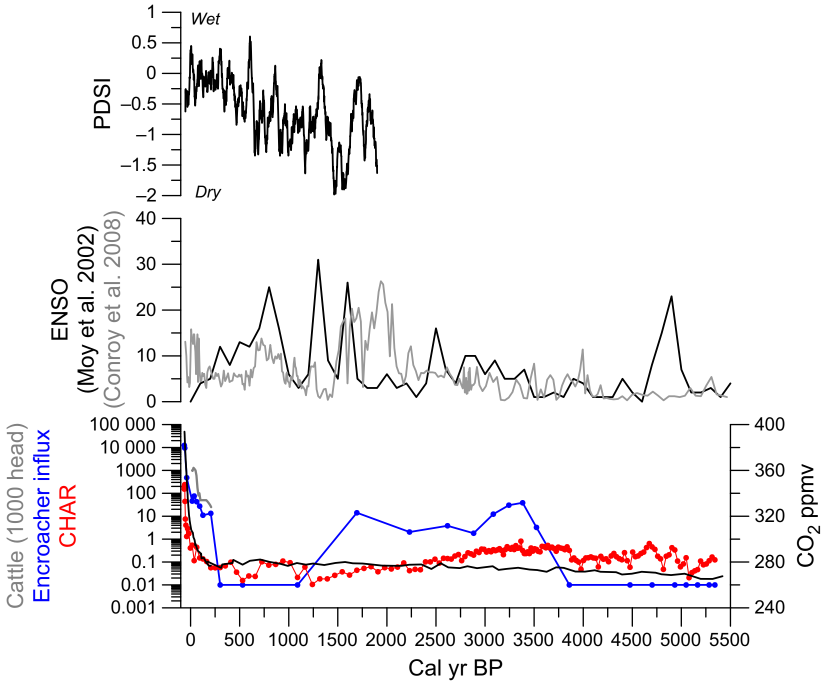

Fig. 2. 5500 yr record of Cloverdale Ciénega and associated proxy. Note the log scale on the lower left hand *y*-axis.

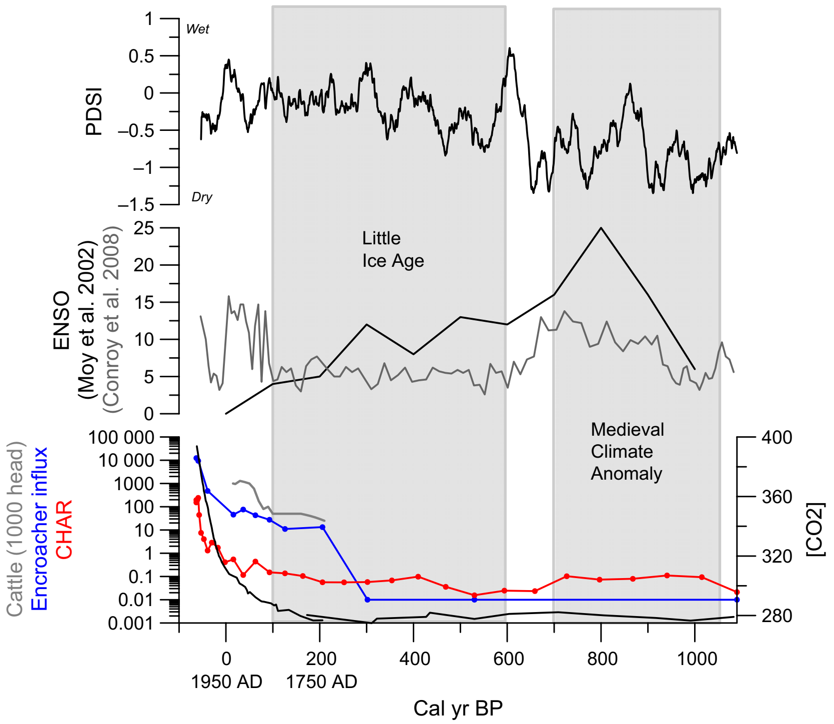

Fig. 3. 1000 yr record of Cloverdale Cienega and associated proxy. Note the log scale on the lower left hand *y*-axis.

H_0: Natural variation

Encroacher taxa are essentially absent from the pollen record from ~5500 cal yr BP to ~3500 cal yr BP. From ~3500 to 1700 cal yr BP these taxa appear at relatively low levels (1–38 grains $cm^{-2}·yr^{-1}$) but are absent again from 1700 to 200 cal yr BP. From 200 cal yr BP (~1750 CE) to the present, encroacher taxa exponentially increase, reaching levels unprecedented over the last 5500 cal yr BP (>12 000 grains $cm^{-2}·yr^{-1}$).

H_1: Climate change

The PDSI represents drought events (Cook et al. 2004) that extend back to 2000 cal yr BP. The trend over the last 2000 yrs is one of increasing moisture with decadal-scale fluctuations between wet and dry conditions. There is a step-wise increase in moisture conditions at ~700 cal yr BP (1300 CE).

The ENSO records come from southern Ecuador (Moy et al. 2002) and from the Galapagos (Conroy et al. 2008). While there are similarities in the data, they are not in complete agreement. For example, Moy et al. (2002) indicate a peak in ENSO activity at ~5000 cal yr BP that is not recorded in the Conroy et al. (2008) time series. Also, the Conroy et al. (2008) data indicate peaks of ENSO activity between 1866–1950 CE and 1990–2004 CE that are not evident in the Moy et al. (2002) data set.

H_2: Changes in CO_2 concentration

Carbon dioxide (ppmv) data from the Mauna Loa observatory and EPICA and Siple Station cores are relatively constant for most of the last 5500 cal yr BP. The CO_2 begins increasing around 200 cal yr BP (~1750 CE) and then accelerates to an exponential rate towards the present.

H_3: Changes in fire regime

Charcoal accumulation rates (charcoal influx, CHAR) are relatively consistent over most of the last 5500 cal yr BP, although slightly higher from the period 5500–2500 than 2500–150 cal yr BP. In the last 150 cal yr BP (since 1800 CE), charcoal influx has increased exponentially.

H_4: Grazing

Specific numbers for grazing intensity for southwestern New Mexico are not available, however from 1850 to 1930 CE cattle numbers in New Mexico in general rose from near zero to 1.3 million head (Culbert 1941). Additional grazing pressure would come from sheep and other pastoral animals (Bahre 1995).

Discussion

While the causes of the woody encroachment of Madrean woodlands into Southwestern grasslands have been long debated (Grover & Musick 1990; Idso 1992; Bahre 1995; Van Auken 2000, 2009), prior research has not examined or compared the possible drivers and ecosystem responses over a time period exceeding Euroamerican occupation of the desert Southwest. One of the strengths of the paleoecological record is the ability to discern the natural range of variability of a given ecological system. Using the sedimentary record of environmental change from Cloverdale Ciénega in southwestern New Mexico, we are able to compare its 5500-yr record of vegetation composition and fire history to atmospheric CO_2 concentration data and climate reconstructions to identify the timing and potential causes of woody plant encroachment.

H_0: Natural variation

The first hypothesis examined is that woody encroachment into the grassland communities is simply a representation of long-term variability. The long-term vegetation record from Cloverdale Ciénega demonstrates that for most of the last 5500 yrs little-to-no woody taxa contribute to the pollen spectra (Figs 2 and 3). The period from ~3500 to 1700 cal yr BP shows evidence of a slight increase in woody encroacher taxa (between 1 and 38 grains $cm^{-2·}yr^{-1}$), suggesting, at best, localized populations of woody plant taxa in a dominant grassland matrix. Significant increases in woody taxa pollen (exceeding 12 000 grains $cm^{-2·}yr^{-1}$) occur in a step-wise pattern during the latest part of the record (the last 250 yrs; Fig. 2). The initial part of this significant rise occurs ~200 cal yr BP during the Little Ice Age (LIA; Fig. 3), a period of cooler and wetter conditions in the Southwest, and appears similar in magnitude to the increase in woody taxa ca. 3500 cal yr BP (Fig. 2). In the last ~150 yrs of the record, encroacher taxa abundance is unprecedented for the 5500-yr paleoenvironmental record, including during the Medieval Climate Anomaly, a period of warmer and wetter conditions in the Southwest (~900–1300 CE). The natural range of variability of woody taxa pollen influx prior to Euro American settlement is between 0.01 and 10.0 grains $cm^{-2}·yr^{-1}$, leading us to reject the hypothesis that recent woody taxa encroachment (10 000 grains $cm^{-2}·yr^{-1}$) reflects the range of natural variability at Cloverdale Ciénega.

H_1: Climate change

Changes in the abundance of woody taxa in the desert grassland ecosystem may have been related to changes in climate, such as long-term droughts ($H_{1.1}$) or variations in the seasonality of precipitation caused by fluctuations in the occurrence or strength of ENSO ($H_{1.2}$). Water availability (drought) has long been linked to the oscillations between grass and woody plant dominance in arid and semi-arid environments (Walter 1971; Tinley 1982; Polley et al. 1997), however, the exact mechanism is still being discussed and debated (van Langevelde et al. 2010). Operating under the assumption that drought may be a possible driver for the encroachment of woody taxa in the desert Southwest, drought data for the past ~2000 yrs were examined in conjunction with the sedimentary pollen record (Figs 2 and 3). PDSI reconstructions show high-amplitude changes during drier-than-present conditions prior to 1250 cal yr BP, when woody encroachers were relatively high (10 grains $cm^{-2} \cdot yr^{-1}$; Fig. 2). PDSI variability decreased from 1250 to 600 cal yr BP, however reconstructed values still suggest relatively dry conditions, when woody encroacher abundance had decreased to near zero (Fig. 2). PDSI reconstructions suggest relatively infrequent drought during the LIA and when woody encroacher abundance began to rise again at 200 cal yr BP. While woody encroacher taxa do increase post LIA, based on the longer-term record of drought from the PDSI reconstruction this is likely not due to changing climate but other variables changing at the same time (see below).

Changes in ENSO over the last 5500 yrs do not correspond to trends in woody taxa encroachment at Cloverdale Ciénega. While we cannot definitively rule out a relationship between climate and woody taxa based on the data presented here, our data indicate that the recent exponential increase in woody taxa is not related to drought or ENSO variability.

H_2: Changes in CO_2 concentrations

Increased concentrations of atmospheric CO_2 are identified as a potential contributor to woody plant encroachment into grassland and savanna ecosystems (Polley et al. 1997; Morgan et al. 2007; Bond & Midgley 2012). The main mechanism for this impact is related to the effect of increased CO_2 on grass stomatal closure and transpiration on water availability (Polley et al. 1997). When CO_2 is more abundant, grasses reduce transpiration, leaving more water available for other plants. Water then can be available to plants growing in the rooting space of the grasses, or as deep water when 'extra' water percolates to deeper soil layers. On woodland/grassland ecotones or in matrices of mixed woodland/grassland this additional water can allow the expansion of woody plants at the expense of grasses.

CO_2 concentrations were stable during the early (~3500–1700 cal yr BP) increase in woody taxa and likely not related to the slight increase in woody taxa at that time (Fig. 2). From 200 cal yr BP (~1750 CE) to the present, encroacher taxa exponentially increased, reaching levels unprecedented over the last 5500 cal yr BP (exceeding 12 000 grains $cm^{-2} \cdot yr^{-1}$). Coincident with the exponential increase in the influx of woody encroacher pollen is an increase in CO_2 concentration. The contemporaneous increase in woody taxa and CO_2 concentration suggests that the increase in abundance of woody plants at ~1750 CE may be attributable to increased levels of CO_2 in the atmosphere associated with the onset of the Industrial Revolution. It has long been recognized that abundance of woody plant taxa increases with increases in CO_2 concentration (Idso & Quinn 1983) and, in fact, elevated CO_2 concentrations favour shrubs at the expense of grasslands (Idso 1992; Polley et al. 1997). However, the earlier pollen influx increase in woodland taxa was independent of CO_2 fluctuations, suggesting that the correlative increases in CO_2 and woodland taxa late in the record is coincident not causative.

H_3: Changes in fire regime

It has also been proposed that fire suppression associated with Euroamerican settlement caused the increase in woody taxa encroachment in southwestern desert grasslands (Van Auken 2000, 2009). Sedimentary charcoal influx (CHAR) is relatively stable throughout most of the record. Again, the early, slight increase in woody taxa at ~3500–1700 cal yr BP had no associated increase or decrease in CHAR. Like CO_2, this is suggestive of changes in woody taxa abundance not related to changes in fire regime. CHAR increases at 1887 CE and is temporally associated with the increase in influx of woody encroachers and CO_2. This increase in CHAR at 1887 CE exceeds the pre-industrial record average. At the same time as CHAR increases, the influx of woody taxa exceeds the influx of any previous value for the entire record. This increase in CHAR associated with the exponential increase in woody taxa not only indicates that fire suppression is not responsible for the increase, but that fire frequency and/or size is increasing coincidently with the woody taxa. It is also possible that increased charcoal is a product of the increased fuel base provided by woody plants. Either way, the abundance of charcoal indicates fires were occurring in the landscape, and we reject the hypothesis that fire suppression resulted in woody plant encroachment in the Southwest.

H_4: Grazing

Increases in CHAR along with woody taxa at 1887 CE are significant because in the late 1800s large herds of sheep and cattle were being moved into the area, and by 1885 there were already nearly 800 000 head of cattle on the landscape (Culbert 1941; Bahre 1995). While the 1887 CE increase in woody taxa and CHAR are closely linked temporally to grazing, this timing is also coincident with the end of the LIA. Bahre (1995) suggests that because the onset of grazing and the end of the LIA are coincident, it is impossible to separate them as causes of the woody encroachment. However, review of the PDSI data for this time period (Fig. 3) suggests that dry conditions at the end of the LIA were not unprecedented or sustained. The PDSI for this region during the LIA was generally stable, with a trend toward wetter conditions, and following the LIA there were periods of even wetter than previous conditions as well as a short drought. If the climate change associated with the LIA was the cause of the recent woody plant encroachment at Cloverdale Ciénega, we would expect woody plants to have increased during previous and more profound droughts such as those prior to 600 cal yr BP (Fig. 3).

The first increase in woody plant pollen influx occurs before grazing was introduced in the desert Southwest (between the samples at 1648 and 1744 CE). Because of the resolution of the data (nearly 100 yrs between samples) it is not possible to know when the encroacher influx increased. It is possible that the increase in encroacher taxa is associated with an increase in CO_2 concentrations related to the Industrial Revolution (Fig. 3), since the first elevated value in encroacher taxa occurs at ~1750 CE. However, the increases in CO_2 at this time are small and do not begin the exponential increase until about 100 yrs later. A second, and more profound, increase in woody plant taxa occurs between the samples dated 1857 and 1887 CE, where woody plant encroacher pollen influx doubled, and then continued to increase toward the present (Fig. 3), coincident with higher CO_2 values and large increases in cattle.

The relationship between grazing and woody plant encroachment is not unexpected, and grazing is considered one of the leading causes of conversion of desert grassland to woodland (Grover & Musick 1990; Van Auken 2000, 2009). Grazing, particularly overgrazing, favours woody plants through several mechanisms. When grasses are reduced or removed, ecological openings are created for woody taxa. Lack of predation and increased access to resources allows these woody seedlings to be more successful. Damage to the soil can also reduce the success of grass seedlings, in that cattle and sheep hooves can facilitate the removal or compaction of those layers critical for grass establishment. In addition to the direct effects of livestock grazing on woody plant encroachment, grazing is also implicated in shrub encroachment through its possible indirect effects on fuel availability and continuity due to consumption and trampling (Crawley 1997; Knapp et al. 2008; Van Auken 2009).

Summary and Conclusions

Based on the multiple working hypotheses for woodland encroachment, natural variation related to climate, changes in CO_2 concentrations, changes in fire regime and grazing, we are able to reject any suggestion that changes in the natural system has caused the encroachment of Madrean woodlands into the grassland communities. Most encroachment can be attributed to anthropogenic activities that have either changed atmospheric composition and/or the fundamental ecology of the grasslands. These changes could be due to changing disturbance regimes (fire, trampling, grazing), and/or competitive exclusion, where selection by grazers allows for the establishment of woody taxa that are not desirable forage. Regardless of the causative factors, our study suggests the expansion of Madrean woodlands into the desert grasslands is unprecedented compared to the previous 5500 yrs.

The results presented here illuminate the causes of historic woody plant encroachment into desert grasslands. The data suggest that the earliest increases in woody taxa are associated with increased concentrations of CO_2 temporally consistent with the Industrial Revolution. A second increase in encroachers is closely temporally correlated to the onset of large-scale grazing in the American deserts. It does not appear that climate, as represented by ENSO and PDSI records, is related to the exponential increases in woody taxa and charcoal production in these systems. While the data here are compelling, further research on additional high-resolution long records across the Southwest is needed to further test and address these hypotheses.

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References

Archer, S., Boutton, T.W. & Hibbard, K.A. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schulze, E.-D., Heimann, M., Harrison, S., Holland, E., Lloyd, J., Prentice, I. & Schimel, D. (eds.) *Global* *biogeochemical cycles in the climate system*, pp. 115–138. Academic Press, San Diego, CA, US.

Bahre, C.J. 1995. Human Impacts on the Grasslands of Southeastern Arizona. In: McClaran, M.P. & Van Devender, T.R. (eds.) *The desert grassland*, pp. 230–264. University of Arizona Press, Tucson, AZ, US.

Bell, H.M. & Dyksterhuis, E.J. 1943. Fighting the mesquite and cedar invasion on Texas ranges. *Soil Conservation* 9: 111–114.

Blaauw, M. 2010. Methods and code for 'classical' age-modeling of radiocarbon sequences. *Quaternary Geochronology* 5: 512–518.

Bond, W.J. & Midgley, G.F. 2012. CO_2 and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Royal Society B* 367: 601–612.

Bowman, D.M.J.S., Murphy, B.P. & Banfai, D.S. 2010. Has global environmental change caused monsoon rainforests to expand in the Australian monsoon tropics? *Landscape Ecology* 25: 1247–1260.

Brown, D.E. (ed). 1982. Biotic communities of the American Southwest – United States and Mexico. *Desert Plants* 4: 1–342.

Buffington, L.C. & Herbel, C.H. 1965. Vegetational changes on a semidesert grassland range from 1858–1963. *Ecological Monographs* 35: 139–164.

Burgess, T.L. 1995. Desert grassland, mixed shrub savanna, shrub steppe, or semidesert scrub? The dilemma of coexisting growth forms. In: McClaran, M.P. & Van Devender, T.R. (eds.) *The desert grassland*, pp. 31–67. University of Arizona Press, Tucson, AZ, US.

Conedera, M., Tinner, W., Neff, C., Meurer, M., Dickens, A.F. & Krebs, P. 2009. Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. *Quaternary Science Reviews* 28: 555–576.

Conroy, J.L., Overpeck, J.T., Cole, J.E., Shanahan, T.M. & Steinitz-Kannan, M. 2008. Holocene changes in eastern tropical Pacific climate inferred from a Galápagos lake sediment record. *Quaternary Science Reviews* 27: 1166–1180.

Cook, E.R., Woodhouse, C.A., Eakin, C.M., Meko, D.M. & Stahle, D.W. 2004. Long-term aridity changes in the Western United States. *Science* 306, No. 5698, 1015–1018.

Crawley, M.J. 1997. Plant-herbivore dynamics. In: Crawley, M. (ed.) *Plant ecology*, pp. 401–474. Blackwell Science, Oxford, UK.

Culbert, J.I. 1941. Cattle industry of New Mexico. *Economic Geography* 17: 155–168.

Dameron, W.H. 1939. Prickly pear eradication and control. *Texas Agricultural Experimental Station Bulletin* 575: 55.

Davis, G.P., Carmony, N.B. & Brown, D.E. 1982. *Man and wildlife in Arizona*. Arizona Game and Fish Department, Phoenix, AZ, US.

Davis, O.K., Minckley, T., Moutoux, T., Jull, T. & Kalin, B. 2002. The transformation of Sonoran Desert wetlands following the historic decrease of burning. *Journal of Arid Environments* 50: 393–412.

Erdtman, G. 1969. *Handbook of palynology: morphology, taxonomy, ecology. An introduction to the study of pollen grains and spores*. Hafner, New York, NY, US.

Faegri, K., Kaland, P.E. & Kzywinski, K. 1989. *Textbook of pollen analysis*. Wiley, New York, NY, US.

Grover, H.D. & Musick, B. 1990. Shrubland encroachment in southern New Mexico, USA: an analysis of desertification processes in the American Southwest. *Climatic Change* 17: 305–330.

Hastings, J.R. 1959. Vegetation change and arroyo cutting in Southeastern Arizona. *Journal of the Arizona Academy of Science* 1: 60–67.

Hendrickson, D.A. & Minckley, W.L. 1985. Ciénegas – Vanishing climax communities of the American Southwest. *Desert Plants* 6: 131–175.

Hicks, S. & Hyvärinen, H. 1999. Pollen influx values measured in different sedimentary environments and their palaeoecological implications. *Grana* 38: 228–242.

Idso, S.B. 1992. Shrubland expansion in the American Southwest. *Climatic Change* 22: 85–86.

Idso, S.B. & Quinn, J.A. 1983. *Vegetational redistribution in Arizona and New Mexico in response to a doubling of the atmospheric CO2 concentration*. Climatological Publications: 17. Arizona State University, Tempe, AZ, US.

Kapp, R.O., Davis, O.K. & King, J.E. 2007. *Pollen and spores*. American Association for Straigraphy Palynologists, Texas A&M University.

Knapp, A.K., Briggs, J.M., Collins, S.L. & Archer, S.R. 2008. Shrub encroachment in North American grasslands: shfits in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology* 14: 615–623.

van Langevelde, F., Tomlinson, K., Barbosa, E.R.M., de Bie, S., Prins, H.H.T. & Higgins, S.I. 2010. Understanding tree–grass coexistence and impacts of disturbance and resource variability in savannas. In: Hill, M. & Hanan, N. (eds.) *Ecosystem function in savannas: measurement and modeling at landscape to global scales*, pp. 257–268. Taylor & Francis, Boca Raton, FL, US.

Marshall, R.M., List, M. & Enquist, C. 2006. *Ecoregion-based conservation assessments of the Southwestern United States and Northwestern Mexico: a geodatabase for six ecoregions, including the Apache Highlands, Arizona-New Mexico Mountains, Colorado Plateau, Mojave Desert, Sonoran Desert, and Southern Rocky Mountains*, pp. 37. The Nature Conservancy, Tucson, AZ.

McClaran, M.P. 1995. Desert grasslands and grasses. In: McClaran, M.P. & Van Devender, T.R. (eds.) *The desert grassland*, pp. 1–30. University of Arizona Press, Tucson, AZ, US.

Mearns, E.A. 1907. *Mammals of the Mexican boundary of the United States: a descriptive catalogue of the species of mammals occurring in that region; with a general summary of the natural history, and a list of trees*. Government Printing Office, Washington, DC, US.

Mehringer, P., Blinman, E. & Petersen, K. 1977. Pollen influx and volcanic ash. *Science* 198: 257–261.

Minckley, T.A. & Brunelle, A. 2007. Paleohydrology and growth of a desert ciénega. *Journal of Arid Environments* 69: 420–431.

Minckley, T.A., Clementz, M., Brunelle, A.R. & Klopfenstein, G.A. 2009. Isotopic analysis of wetland development in the American Southwest. *The Holocene* 19: 737–745.

Minckley, T., Brunelle, A. & Turner, D. 2013. Paleoenvironmental Framework for Understanding the Development, Stability, and State-Changes of Ciénegas in the American Deserts. USDA Forest Service Proceedings RMRS-P-67.

Monnin, E., Steig, E.J., Siegenthaler, U., Kawamura, J., Schwander, J.J., Stauffer, B., Stocker, T.F., Morse, D.L., Barnola, J.M. (…) & Fischer, H. 2004. Evidence for substantial accumulation rate variability in Antarctica during the Holocene, through synchronization of CO2 in the Taylor Dome, Dome C and DML ice cores. *Earth and Planetary Science Letters* 224: 45–54.

Morgan, J.A., Milchunas, D.G., Lecain, D.R., West, M. & Mosier, A.R. 2007. Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in the shortgrass steppe. *Proceedings of the National Academy of Sciences of the United States of America.* 104: 724–729.

Moy, C.M., Seltzer, G.O., Rodbell, D.T. & Anderson, D.M. 2002. Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene epoch. *Nature* 420: 162–165.

Neftel, A., Friedli, H., Moor, E., Lötscher, H., Oeschger, H., Siegenthaler, U. & Stauffer, B. 1994. *Historical CO2 record from the Siple Station ice core*. Carbon Dioxide Information Analysis Center, Oak Ridge, TN, US.

Parker, K.W. & Martin, S.C. 1952. *The mesquite problem on southern Arizona ranges*. U.S. Department Circular, 78p.

Polley, H.W., Mayeux, H.S., Johnson, H.B. & Tischler, C.R. 1997. Viewpoint: atmospheric CO_2, soil water, and shrub/grass ratios on rangelands. *Journal of Range Management* 50: 278–284.

Tans, P. & Keeling, R. NOAA/ESRL (www.esrl.noaa.gov/gmd/ccgg/trends/) Scripps Institution of Oceanography (scrippsco2.ucsd.edu/) (accessed 17 July 2013).

Tinley, K.L. 1982. The influence of soil moisture balance on ecosystem patterns in southern Africa. In: Huntley, B.J. & Walker, B.H. (eds.) *Ecology of tropical savannas*, pp. 175–192. Springer, Berlin, DE.

Traverse, A. 1994. *Sedimentation of organic particles*. Cambridge University Press, Cambridge, UK.

Van Auken, O.W. 2000. Shrub invasions of North American semi-arid grasslands. *Annual Review of Ecological Systems* 31: 197–215.

Van Auken, O.W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* 90: 2931–2942.

Walter, H. 1971. *Ecology of tropical and subtropical vegetation*. Oliver and Boyd, Edinburgh, UK.

Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Cloverdale Ciénega Vibracore Description (CC08C).

Fig. S1. Cloverdale Cienega age model, using a smoothing spline (0.10 smoother; goodness of fit = 22.4).

Fig. S2. Pollen percentage diagram from Cloverdale Ciénega. Stippled shading indicates an exaggeration of 5X. Dots indicate the presence of a single pollen grain.

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