RESEARCH ARTICLE

Livestock and grassland interrelationship along five centuries of ranching the semiarid grasslands on the southern highlands of the Mexican Plateau

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Native grasslands worldwide have been degraded by grazing, but the processes involved have been studied insufficiently. Grasslands were a major habitat on the southern section of the Mexican Plateau when the Spaniards arrived 500 years ago. Since then, they have been impacted heavily through grazing, but the details and history of such impacts have not been established. We aimed at untangling almost 500 years of grazing of these grasslands, based on extensive searches of published information and of documents in historical archives. We identified three periods of ranching: Cattle, from the mid-16th to the mid-17th Centuries; sheep, reflecting a change from tall to short grasses; and, finally, goats and horses, along with sheep, asses and some cattle, after serious grassland degradation by the mid-20th Century. Overgrazing has impacted grassland composition in the region and its capacity to support livestock, but also, strongly affect some 20 species of native vertebrates and an unknown number of plant and invertebrate species. The current condition of some ranges and a livestock exclosure indicate that grassland improvement is possible, but realistic objectives based on biodiversity conservation and livestock production should be targeted, rather than utopic pre-livestock frameworks. Grasslands in the region at the time of Spanish arrival possibly had a mixture of grasses and herbs, but buffalo grass and the central Mexico tobosa grass are potential initial range management targets for grassland recovery of the ranges in worst condition, while blue gramma and the Mexican plateau gramma are good targets for ranges that still have some grass cover.

Keywords: Landscape history; Overgrazing; Grazing; Environmental degradation; Conservation; Llanos de Ojuelos

Dedicated to the memory of Vicente Ferreira (1952–2017).

Introduction

Zooming in from space to 21°45'32" Lat N, 101°38'33" Long W shows the square, dark patch in the midst of lightcolored surroundings visible in **Figure 1**. The dark patch is a 1-hectare plot from which all grazing by livestock has been excluded since 1980. The surroundings comprise open rangeland where horses, asses, sheep, goats, and a few cattle graze, and by some dry-farmed agricultural plots. Before the exclosure was established, the site looked the same as the surrounding open range, and both areas looked

Correspondence author: Mónica E. Riojas-López (monica.riojas@academicos.udg.mx) much the same as the non-excluded area looks nowadays (EM, pers, obs.). In 2017, nearly 4 decades after the fence was installed, the areas outside and inside the exclusion were noticeably different, as seen in Figure 2. Those outside it had a ground cover of 53% and were visually dominated by jimmyweed (Isocoma veneta) and cespitose forms of gramma grasses, whereas inside the exclosure 99% of the ground was covered by a tall (~60 cm high) and dense herbaceous community of plants, in which purple muhly (Muhlenbergia rigida) was the major grass component, followed by gramma grasses (Bouteloua spp.) and forbs (David Almanzor-Rojas and MER-L, unpub. data). The contrast between plant cover and composition inside and outside the exclosure suggests strongly that the grasslands found in the area before livestock was brought in the 16th Century were very different from those found today.

The Llanos de Ojuelos, where the cattle exclusion is located, is part of the southernmost extension of the North American prairie ecosystem. To the northwest of it, not far, lush grasses were said to be tall enough to touch the bellies of horses (Crosby, 1972). In the Llanos de Ojuelos itself,

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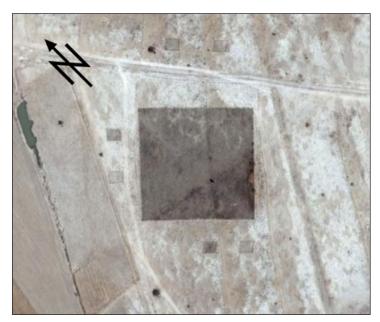


Figure 1: One-hectare livestock exclosure (dark square; 21°45'32" Lat N, 101°38'33" Long W) established in 1980 near Vaquerías, Jalisco, Mexico (Google Earth, ©2018 DigtalGlobe. Image date: 17/01/2011). The dark exclosure contrasts with the much lighter surroundings, reflecting its higher ground cover by herbaceous plants. Small darker squares are more recent experimental plots. DOI: https://doi.org/10.1525/elementa.416.f1



Figure 2: Livestock exclosure (upper) and its immediate surrounding range (lower), near Vaquerías, Jalisco, Mexico in February 2017 (photographs: David Humberto Almanzor-Rojas, July 2017). When the exclosure was established, in 1980, both it and the surrounding area had the same plant cover as the later has currently. In 2017, 99% of the ground inside the exclosure was covered by a ~60 cm high and dense herbaceous community, while the area outside the exclusion had a ground cover of 53% and was visually dominated by jimmyweed (*Isocoma veneta*) and cespitose forms of gramma grasses (*Bouteloua* spp.). DOI: https://doi.org/10.1525/elementa.416.f2 the hacienda of San Juan de los Herrera, about 10 km SE of Pinos, Zacatecas, had been grassland (Reyes, 2002), and at the end of the 18th Century there were "…immense grasslands…" in the lands of the hacienda Ciénega de Mata, at the convergence of the states of Jalisco, Aguascalientes, and Zacatecas (Gómez Serrano, 1984; placing of all locations mentioned are given in the Supplementary material). The transformation of the lush grasslands encountered by the Spaniards in the 16th Century into the bleak ranges they are now has been blamed on overgrazing by livestock (Riojas-López and Mellink, 2005).

Overgrazing, a widespread cause of landscape transformation (Webb and Stielstra, 1979), is a complex process that is especially pernicious as its time scales, longer than a human lifetime, make it largely imperceptible (Archer, 1989; Schlesinger et al., 1990; Manzano et al., 2000; Mellink and Contreras, 2014; Archer et al., 2017). Basically, when grazing overwhelms the capacity of the preferred plants to stand it, these lose competitive ability against other, less desired plant species whose abundances increase in the range. If this is continued, other plants even less desirable for livestock that were not originally present, appear. Besides reducing the competitive potential of their preferred plant species, non-indigenous livestock disperse the seeds of invading species, especially shrubs and trees whose pods they eat. When doing so, livestock not only transport the seeds, but often increase their germination rate through scarification in the gut (Gutiérrez and Armesto, 1981). Long term grazing also causes an increase in spatial and temporal heterogeneity of water and nutrients. As a result of all these processes, some of the most evident manifestations of advanced overgrazing are the encroachment of shrubs and trees on formerly homogeneous grasslands (Schlesinger et al., 1990; Bahre and Shelton, 1993; Bock and Bock, 2000; Van Auken, 2000; Archer et al., 2017).

Furthermore, in grasslands where shrubs and trees were kept at bay by wildfires, grazing may remove the necessary fuel for wildfires to happen (Leopold, 1924; Archer, 1989; Archer et al., 2017), which can in turn affect plant species that rely on fires (eg. to germinate). Overgrazing promotes also soils erosion by reducing plant cover and by loosening the soil through trampling, while livestock trails can turn into linear arroyos, which further contribute to soil erosion (Scurlock, 1998). In other cases, trampling, especially by sheep, compacts soils heavily, reducing infiltration of rainfall and promoting runoff (Rauzi and Hanson, 1966; Mwendera and Mohamed Saleem, 1997; Sharrow, 2007). Overgrazed rangelands have higher soil temperatures and altered soil moisture relationships (Balling et al., 1998); reduced levels of soil moisture, organic matter, and nitrogen, and altered values of other edaphic productivity parameters (Abril and Bucher, 1999), as well as a lower capacity to store carbon (Conant and Paustian, 2002). In all, overgrazing negatively affects the physical characteristics of the habitats grazed, their biodiversity and individual species, ecosystem functions and services, and organization (Fleischer, 1994).

Changes in the structure and composition of the vegetation caused by overgrazing also affect the animal communities originally present. This has been documented for invertebrates (Debano, 2006), wild birds (Mellink and Valenzuela, 1992; Brown et al., 2012) and wild mammals (McMahan and Ramsey, 1965; Loft et al., 1987; Mellink and Valenzuela, 1995; Eccard et al., 2000). When overgrazing becomes severe, the system can change beyond a transitional threshold, from which it may be very difficult, or impossible to return to its previous stable state (Archer, 1989; Van Auken, 2000).

Due to their degradation by grazing, and also to their conversion to farmland, throughout the world native grasslands are in urgent need of conservation and/or restoration measures (Hoekstra et al., 2005). However, despite the known consequences of overgrazing for biological conservation and for livestock ranching, the processes involved have been studied insufficiently and often through poorly designed and short-term studies (Jones, 2000; Dettenmaier et al., 2017).

Like other arid and semiarid lands throughout the world, those in northern Mexico are widely overgrazed (Aguado-Santacruz and García-Moya, 1998; Riojas-López and Mellink, 2005; Yeaton and Flores, 2006; Medina-Roldán et al., 2007; Ceballos et al., 2010; Manzano et al., 2000; Perramond, 2010; Mellink and Contreras, 2014), but little information exists on the process beyond the presumed consequences on plant composition.

In the southern portion of the semiarid Mexican Plateau, almost 500 years of grazing by livestock have elapsed. While the history of the Mayorazgo de Rincón Gallardo, a huge land possession in the area (mid 18th to late 19th Centuries), and the hacienda of Ciénega de Mata, one of its components, has been the subject of several books, the history of grazing has not been analyzed; much less have the relationships between livestock history and grassland condition been explored. As different livestock species, having different ways of foraging, are suited better for different types of range (Larson et al., 2015), the history of livestock changes can offer clues to the history of changes in range conditions.

The region is highly anthropized and with no formal conservation actions, other than hunting regulations. Establishment of protected areas is not a regional option, as most of the land is already transformed, thus other forms of conservation of biodiversity must be designed. To this end, we have engaged in the reconstruction of the history of the region's natural landscape since the arrival of the Spaniards, and of the processes involved, to offer objective foci for conservation.

As part of this effort we focused on one of the prominent landscape features, the grasslands. Popular and technical "wisdom" based on 19th Century lore have always contended that the natural condition of the rangelands is that of "sheep grasses". In agreement, some research efforts developed a few decades ago were focused on restoring to that state. However, we are convinced that simple degradation between the 19th Century and late 20th Century is not the whole story, and that if we are to make rational decisions about range restorations we must be aware of the much longer history.

As opposed to reductionist and short-time perspectives of overgrazing, the analysis of the process of grassland degradation under a wide historic perspective can provide a better reference framework to guide management decisions for grassland restoration based on sound ecologically objectives. Thus, a first step to restore the degraded grasslands of an area is the reconstruction of its matched grassland-livestock history. Aiming at doing so, inasmuch as the data available allowed, we focused on three objectives: (1) Synthesize the history of livestock grazing since their first introduction to the region, (2) link this history with that of the degradation of the regional grasslands, and (3) based on that and the current knowledge of the habitat requirement of grassland wildlife species, infer some of the impacts of overgrazing on them. We selected the Llanos de Ojuelos and surrounding regions, because historically they had large expanses of semiarid grassland (Riojas-López and Mellink, 2005) and because we have long-time research experience and region-wide knowledge of its biota and conservation problems.

Study area

Our study is centered in the Llanos de Ojuelos, in the southern part of the physiographic region known as the Mexican Plateau. This plateau extends from the center in northern Mexico south to the Trans-Mexican Volcanic Belt. The term "Mexican Plateau" can be confusing as it is used in the archeological literature for an entirely different region, to the south, where the large Teotihuacan and Mexica cultures of central-Mexico developed. This later region, the Valley of Mexico, is not part of the physiographical Mexican Plateau.

A second clarification is in order: The term Chichimeca is also a source of confusion. Whereas the term was used by the Mexica to refer to any neighboring tribes that they considered uncivilized, during Colonial times it was redefined to apply only to the hunter-gathering groups in northern Mexico, especially those in the southern Mexican Plateau: Cazcanes, Guamares, Zacatecos and Guachichiles (Mellink et al., 2018b).

Information about the processes of landscape transformation in the Llanos de Ojuelos is extremely scant, and to integrate the history of its grasslands grazing, a wider, regional approach had to be taken. So, our study region, shown in **Figure 3**, includes also the Valle de San Felipe, Valle de San Francisco, Valle de Arriaga, and part of El Llano, at the confluence of the Mexican states of Jalisco, Aguascalientes, Zacatecas, San Luis Potosí, and Guanajuato (approximate extreme coordinates: 21°45' and 22°41' N, 100°84' y 102°19' O; alt. 2200–2350 m above sea level). This region is a tableland with low mountains and valleys (Nieto-Samanniego et al., 2005). Soils of the four eastern valleys are of Quaternary alluvial origin; those of El Llano, the westernmost one, originated from Miocene sandstones and polymictic conglomerates. The

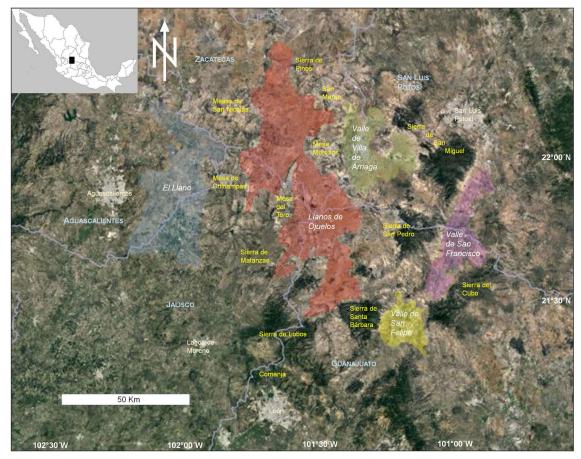


Figure 3: Study area in the southern portion of the Mexican Plateau (background image: Google Earth, ©2018 DigitalGlobe). This image exhibits the valleys in the study region as colored areas with white lettering, while the low mountains are indicated with yellow lettering. Small caps in blue indicate states. Valley delimitation was done by hand. DOI: https://doi.org/10.1525/elementa.416.f3

soils of the valleys are underlain by duripan (locally called "tepetate"). The mountains and hills are formed mostly by Oligocene rhyolites, rhyolitic tuffs and ignimbrites (Servicio Geológico Mexicano, 1997, 1998).

The climate is temperate semiarid, with an annual precipitation between 400 and 700 mm, 80% of which falls between June and September, while between November and April there falls almost no rain (**Figure 4**). Rainfall is highly variable, both in amount and timing, and pan evaporation exceeds precipitation in all months of the year. Mean annual temperature is 16–18°C, with a minimum in January (–2°C) and maximum in May (32°C), and frost episodes from November to April. Major vegetation types in the region are xeric grasslands and shrublands, with dwarf oak (*Quercus* spp.) stands on some mesas and ravines, patches of yucca trees (*Yucca decipiens*), and, the most typical feature of the region, stands of arborescent *nopales* (prickly-pears, *Opuntia* spp.).

Methods

To fulfill our objectives, we reviewed only range livestock grazing species, as the history of pigs and domestic fowl does not help to understand the history of grassland changes. We relied on two main documentary sources that provide information on habitats and the history of ranching in the area. The first one was published literature, including formal books and journal articles, "gray" documents and little known works. These, we searched for in the library system of the Universidad de Guadalajara, the Biblioteca Pública del Estado de Jalisco "Juan José Arreola", the University of California in San Diego, and regional libraries in Aguascalientes, Zacatecas and San Luis Potosí, as well as the authors' personal collections, internet databases and journals. The second source were unpublished documents archived in the Archivo General de la Nación, México, the state historical archives of Jalisco, Aguascalientes, San Luis Potosí, and Zacatecas, the Biblioteca del Estado de Aguascalientes, the Archivo Diocesano del Arzobispado de Guadalajara, Special Collections of the University of California in San Diego, and the Archivo General de Indias, in Seville, Spain. We complemented this with our own work in the region in 1978–1981 and since 1995. To infer the consequences of overgrazing on wildlife we used knowledge on the ecology of the species, as well as our own experience and data, both, published and unpublished.

Results

Colonial period (1542-1821)

Four years after the Spaniards defeated the Mexica, or Aztec, people in 1521, the first sheep set hooves on the Mexican mainland; cattle did so one year later (Matesanz, 1965). A decade later, the Viceroy ordered that cattle be introduced north of the "Valle de Chichimecas" (currently Lagos de Moreno), and in 1532 some Spaniards settled in this valley (Brand, 1961). By 1541, cattle had expanded throughout the plains of northern Mexico (Gerhard, 1982), and in 1542–1545, cattle herdsmen became the first Spaniards to enter the Llanos de Ojuelos region (Chevalier, 1963).

Soon afterwards, silver was discovered in Zacatecas (1546) and Guanajuato (1552) (Florescano, 1969; Meade,

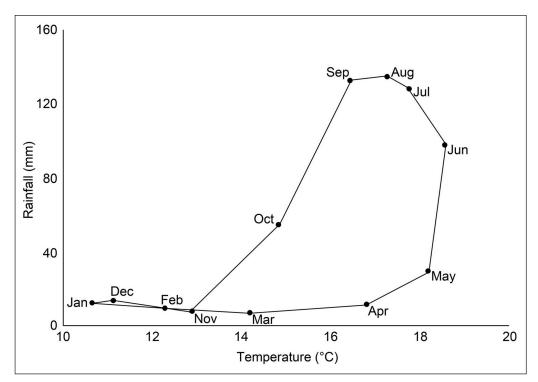


Figure 4: Climograph of the municipality of Ojuelos de Jalisco, Mexico (based on data from the Ojuelos climatic station; 1986–2009). The region has a semiarid climate in which the rainy season is strongly concentrated during the summer months, with no mid-summer drought, and very little rain falls during the winter months. Three climatic seasons can be defined: Dry cold, dry warm, and rainy. DOI: https://doi.org/10.1525/elementa.416.f4

1945; Powell, 1977). These discoveries unleashed Spanish colonization efforts in the southern section of the Mexican plateau. The mines and resulting towns required tallow for candles, soap, and as a lubricant; leather for buckets, ropes, harnesses, shoes, clothing, and other commodities; and meat (Brand, 1961; Florescano, 1969; Morrisey, 1957; Jordan, 1993). To supply these resources, a large cattle center developed north of San Juan del Río, Querétaro (Morrisey 1957), from which further cattle was sent to the Llanos de Ojuelos and nearby areas (de Santamaría, 2000). Along with cattle for meat, tallow and leather, draft animals were brought to the region since the establishment of the first mines as they were needed for the work at them and to transport goods to and from them. However, total numbers of draft animals were proportionally low.

The needs of these mining towns led to the development of roads (Martínez-Saldaña et al., 2009), and between 1551 and 1556 the "Camino Real de Tierra Adentro" (the Royal Road of the Inlands) that linked Zacatecas with the city of México, passing though Lagos de Moreno 65 km to the southwest of Ojuelos, was well traveled (Calvo, 1997; Mota y Escobar, 1940). By then, the raising of livestock had become the second major economic activity of the country (Miranda, 1944), and the México-Zacatecas road became one of the main gateways of livestock to northern Mexico (Martínez-Saldaña et al., 2009). In ensuing decades (1550–1595), the Chichimeca people, especially Zacatecos and Guachichiles, fought a fierce war against the Spaniards (Powell, 1977). Despite it, many "estancias de ganado mayor" (allotments for large stock) were established along the Camino Real (de Mendieta, 1945). As part of the Chichimeca War, the presidio of Ojuelos was established in 1569, and the Camino Real was re-routed northeastwards, favoring cattle ranching in the Llanos de Ojuelos and neighboring areas.

It has been contended that when the Spaniards first arrived to the Valley of Mexico, they encountered a population estimated at 25 million, and that they were successful in conquering them because smallpox killed half the indigenous population (Borah and Cook 1969). This collapse would have not only allowed a military victory, but also caused the emptying of vast expanses of land cleared and prepared for farming, lands that the Spaniards were soon to seize for their farming and grazing. As popular and appealing as the story is, both the population estimate and the severity of the smallpox epidemic have been strongly contested in an enlightening analysis by Francis J. Brooks (1993), who indicated that "[a]lmost every element of this perceived account is false, epidemiologically improbable, historiogaphically suspect, or logically dubious". What can be asserted is that the indigenous human populations in the Valley of Mexico and nearby regions summed some millions and that a mild smallpox epidemic, but not killing a third or half the population, occurred in that area in 1520 or 1521 (Brooks, 1993).

As for the people in the southern part of the Mexican Plateau it is nearly impossible that they were affected by the smallpox epidemic striking the Valley of Mexico. Not only were they >300 km away, but the local groups were hunter-gatherers, mostly nomads or, those in the Tunal Grande, living in neighborhoods of dispersed family homesteads (Mellink et al., 2018b). As far as is known they did not have any contact with the peoples in the Valley of Mexico. Even if a chain of contacts linked them somehow, they would have not received smallpox for two reasons. First, the indigenous people in the Valley of Mexico were struggling with adjusting to their new political, economic and operational reality. Second, smallpox transmits poorly and through person-to- person contact or the inhalation of saliva droplets; infecting primarily household members and friends of the ill, because by the time patients are contagious, they are usually bedridden (https://www.who. int/csr/disease/smallpox/faq/en/, accessed 17 March 2020).

A more likely European disease epidemic infecting native people in the southern part of the Mexican Plateau would have been the 1545 epidemic that struck many places of central and southern Mexico, and has now been indicated as of *Salmonella enterica* (Vågene et al., 2018). This epidemic broadly coincided with the discovery of the Zacatecas and Guanajuato mines. However, its transmission seems little likely among hunter-gatherer humans with no established villages. Indeed, Guillermo de Santamaría's (2000) account about the Guachichiles written two decades later did not comment on any epidemic or disease.

Unlike the valleys of central Mexico (Simpson, 1952) and the plains of northern Zacatecas which soon embraced sheep herding, the Llanos de Ojuelos region remained sheepless (Florescano, 1990; Serrera Contreras, 2015). In 1573, at the border of "Tierra Adentro" (the interior lands) in Nueva Galicia, the land was inhabited only by large stock and their owners and herdsmen (Román Gutiérrez, 2005). A detailed 1579 "Mapa de las Villas de San Miguel y San Felipe de los Chichimecas y el pueblo de San Francisco Chamacuero", of which Figure 5 is an extract corresponding to part of our study area, depicted cattle in the grasslands of the Llanos de Ojuelos and in the Valle de San Felipe, but no small stock. This is consistent with a 1582 complaint from "estancieros" (ranchers) about Guachichiles raiding towns and ranches to steal mares, horses, and "ganados" (Powell, 1997). The term "ganado" is ambiguous, as it can mean any kind of livestock, but in New Spain's colonial documents it usually refers to cattle. Other sources indicate the Guachichiles' taste for cattle, mules, and horses (Torquemada, 1975; de Herrera y Tordecillas, 1728), but not for small stock, reinforcing the idea that no small stock was yet present in the area.

At this time, the areas surrounding the Llanos de Ojuelos and nearby valleys were stocked heavily with cattle, both year-round and for the winter (Florescano, 1990; Parry, 1948; Frye, 2000). By the end of the 16th Century, once the Chichimeca War had come to an end, the area was peopled rapidly, and cattle continued to be the main livestock in the region (Mota y Escobar, 1940; Gómez Serrano and Delgado Aguilar, 2005; Berthe et al., 2008). For example, between 1629 and 1630, at El Tecuán (consisting of 1 "sitio de ganado mayor", a legal unit of land allotment for the raising of large stock, 1756 ha), 8700 calves were reportedly branded, and 400 mares were left after 440

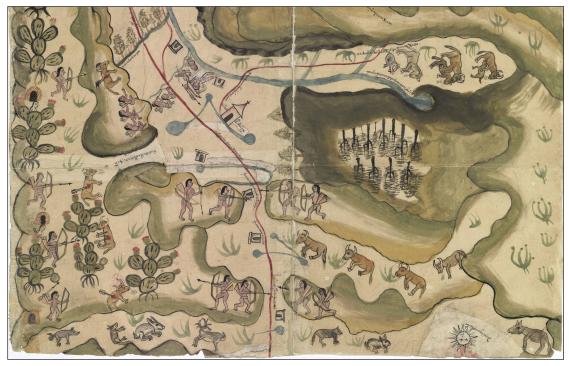


Figure 5: Extract of the "Mapa de las Villas de San Miguel y San Felipe de los Chichimecas y el pueblo de San Francisco Chamacuero". This map, which is archived at the Real Academia de la Historia in Madrid, was elaborated in 1579 by an unknown illustrator. It was possibly drawn elsewhere based on very detailed notes which have not been found. The map is roughly southeast on top-northwest on bottom. The section of the map here reproduced corresponds to the southern part of our study region. The three place names in the title of the map correspond to the current cities of San Miguel de Allende, San Felipe Torres Mochas, and Comonfort in the Mexican state of Guanajuato. DOI: https://doi.org/10.1525/elementa.416.f5

had been removed (Gómez Serrano and Delgado Aguilar, 2005). Some haciendas, like the Hacienda de Ojuelos, continued to produce only cattle for at least another century (*Testimonio de cuentas y relación jurada que dicho Don Cristobal Delgadillo entrega de la Hacienda de Ojuelos*, 20 September 1754, and a similar inventory three years later; Archivo Diocesano del Arzobispado de Guadalajara; Sierra de Pinos, box 1).

In nearby regions, livestock ranches were different. Sheep ranches existed during the mid-16th Century in southern Guanajuato, as shown by the sale of a small stock allotment near San Miguel (AGN/Instancias Coloniales/Mercedes/Vol. 3/15794/15/pages 54 and 54 reverse). In 1570, sheep had already reached the mountains west of our area, as indicated by a Chichimeca raid on a sheep ranch near Colotlán (Román Gutiérrez, 2005). Other areas not far from our study region were soon stocked heavily with sheep, like near the city of San Luis Potosí where sheep production climaxed in 1630 with herds numbering tens of thousands of animals (Frye, 1986, 2000; Esparza Sánchez, 1988 based on Bakewell, 1976).

The first sheep to reach the Americas were of the Churra breed, rustic and primitive sheep of the Iberic Peninsula that are able to use dew and succulent plants as sources of water, and survive days in a row without drinking it in liquid form (Ministerio de Medio Ambiente y Medio Rural y Marino, 2010). Merino sheep were imported later, but the Churra were more convenient and adaptable to the plains of northern Mexico and southern U.S. (Baxter 1993). The rough fleece of the sheep in the region in Colonial times confirms them as Churra. Mutton from this breed is said to have unparalleled flavor, and the little gross wool they produced is well suited to manual processing (Baxter, 1993). The low quality of the wool was an advantage rather than a downside, because, in addition to the mines, "obrajes" (weaving mills) for fabrication of rough, cheap textiles were the only industry allowed by the Spanish Crown, and only because its inability to supply the local demand due to the unprofitability of transporting them to the region (Matesanz, 1965). Although sheep were widely distributed and abundant in the region, and at some places like El Sitio only sheep were raised (del Campo Macías, 2006), in many others, like the haciendas of Espíritu Santo, Ojuelos, Lagos, and Ojocaliente, sheep shared the place with cattle, horses, and mules (de Arteaga, 1990).

Thus, when the time was ripe to change the type of livestock being raised, ranchers in the Llanos de Ojuelos did not have to look far for a suitable alternative, and sheep raising was taken up. Between 1628 and 1652 the Mayorazgo Rincón Gallardo was enlarged with 27.5 allotments for large stock (48,279 ha) and, for the first time, 13 for small stock (10,140 ha). As it was illegal to use allotments for large stock to raise small stock and vice versa, this exhibits a change in local ranching interests. The stimulus for changing to sheep must have been strong, as 17 years later the Mayorazgo requested the addition of 87 allotments for small stock (152,738 ha) and a waiver of

the restriction on stock type that could graze in each type of allotment, both of which were approved by the president of the Audiencia de Guadalajara (Gómez Serrano and Delgado Aguilar, 2005). At least nine detailed inventories of the Mayorazgo's livestock from 1657 to 1734 indicate the overwhelming sheep abundance (**Figure 6**). Sheep remained predominant in the area throughout the 18th Century, and until the turn of the 19th Century (Gómez Serrano and Delgado Aguilar, 2005; Esparza Sánchez, 1988; Serrera Contreras, 1974; Alcaide Aguilar, 2004).

In the late 17th or early 18th Centuries small-scale goat raising commenced in the area (Alcaide Aguilar, 2004). So, while the 1683 Ciénega de Mata livestock inventory does not mention any, that of 1704 included 1533 goats, and by 1734 they accounted for 11% of all livestock inventoried (data in Alcaide Aguilar, 2004). Nevertheless, goats were a small component of regional livestock. In 1756, the livestock at Hacienda de San Pedro de Gogorrón, on the eastern border of our area of interest, included hundreds of draft animals, 1220 cattle, 261 calves, and 1015 meat goats, albeit no sheep (Inventario de toda la Hacienda de San Pedro de Gogorrón en el Obispado de Mechoacán..., Archivo Diocesano de la Arquidiócesis de Guadalajara). By the late 18th and early 19th Centuries, the region supplied a large part of the sheep from "Tierra Adentro" that were herded annually to the fairs and markets on the Central Valley (Serrera Contreras, 1982).

Independent Mexico period (1821-1920)

Sheep raising continued to be the main form of ranching in the region after Mexico obtained its independence from Spain. In 1843, 90% of the income of the Hacienda de Ojuelos was from wool, live livestock, meat, and tallow, and in 1861 it was devoted mostly to sheep, along with farming (Gómez Serrano, 2000). At this time (1844), the Hacienda del Refugio had a flock of several thousand sheep (Gilliam, 1847), and in 1854 or 1855, there were 3000 large livestock, but 75,500 small livestock in Pinos (García y Cubas, 1858). Except for the gross cloth fabrics in Zacatecas and Aguascalientes, and mezcal from Pinos, in the early 19th Century all goods needed in the region had to be brought in (Ward, 1828). Hence, an intensive traffic of commodities existed, which required abundant draft and train animals. In 1827 between San Jacinto and Aguascalientes, the farmlands were interspersed with pastures with oxen, while the marquis of Guadalupe had 18,000 breeding horses in Ciénega de Mata (Ward, 1828). Draft animals were required not only for farming and for the transport of commodities, but importantly as work force for the mines: for example, still in the early 19th Century the entire machinery of the Zacatecas mines was moved by mules (Ward, 1828).

Goats continued to be important on ranches at the eastern side of our study region, as they were in 1756. In 1822 the peasants at El Rincón, down from the Sierra de Guanajuato on the road to San Felipe, lived by raising goats (Poinsett, 1825), and around 1827 the haciendas of the marquis of Jaral not only provided 30,000 sheep every year to the market of Mexico City, but slaughtered a similar number of goats at his Hacienda de Jaral for tallow and skins (Ward, 1828).

Goat production started moving west and had become important in Ojuelos in 1878 (C. Riojas López, 2003). Despite this western "move" of goats, elsewhere in the area, sheep continued to be the major livestock. By 1889 the sheep population in Pinos had increased to 242,500 "rams" (likely misused for sheep), in contrast with 3200 goats, 18 600 cattle, and 7150 horses, a few mules, hinnies, and asses, making this municipality one of the most important sheep areas in the state of Zacatecas (Bonilla, 1889).

Post-Revolutionary period (1920 to date)

The Mexican Revolution (1910–1920) did not affect directly the Llanos de Ojuelos and neighboring areas, but land reform following it caused major regional changes in land ownership and soil occupation. Many rangelands were plowed for farming, which lead to increases in the

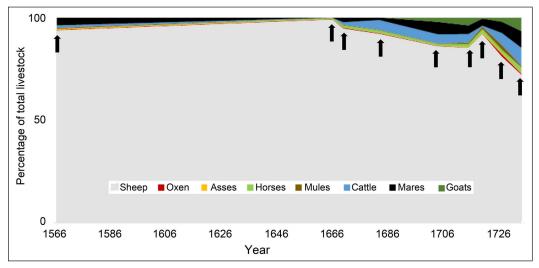


Figure 6: Composition of the herd at Ciénega de Mata from 1657 to 1734 (drawn from data in Alcaide Aguilar 2004). This synthesis of hacienda inventories exhibits the period of absolute sheep dominance in the area, up to the late-17th Century, when other groups of livestock began to increase in numbers. The black arrows indicate the times of the inventories. DOI: https://doi.org/10.1525/elementa.416.f6

need of work animals. These, particularly horses and mules, had become scarce in the early 20th century, at least in Pinos (Esparza Sánchez, 1988), but soon their numbers increased as a response to the demand. In Pinos, the population of horses, asses and mules increased from 18,397 to 24,526 between 1930 and 1940 (de la Peña, 1948). Here and elsewhere in central Zacatecas mule farms were established to supply the need of draft animals for plough, cart, and carriage (de la Peña, 1948). Asses were also yoked to the plough, especially by farmers who had received land but lacked oxen or mules. They were also pack animals to transport charcoal and firewood (de la Peña, 1948).

Despite the declared importance of goat production in Ojuelos in the late 19th Century, goats did not seem to become a major component of the regional livestock until well into the 20th Century, soon after the land redistributions that followed the Mexican Revolution. The municipalities of Villa Hidalgo and Pinos became major producers of goats in the state of Zacatecas (de la Peña, 1948). According to official agriculture and livestock censuses, in 1930 there were about twice as many goats as sheep in the entire state of Zacatecas (González and Scheffey, 1964). In Pinos the sheep herd grew from slightly over 45 000 in 1930 to more than 67 000 in 1940, while the number of goats diminished from about 94 000 to about 61 000 in the same period (de la Peña, 1948). This pattern was seen throughout the state of Zacatecas, where in 1960 there were 1 136 950 sheep vs. 1 101 839 goats (González and Scheffey, 1964). Herd composition was not uniform across population segments. For example, in the 1940s, large landowners in Pinos raised sheep and horses, while small ranchers and ejidatarios (peasants with rights to communal land) emphasized cattle and goats (de la Peña, 1948). Whether this was a response to differences in the quality of their respective landholdings has not been analyzed.

Between 1960 and 1976 the national sheep herd shrunk 29%, according to the bylaws of the "Instituto Nacional de Ovinos y Lanas" (INOL; National Institute of Sheep and Wool; Antonio Gómez, pers. com.). In 2007, according to the national census, there were almost 70 913 sheep and 42 320 goats in Pinos. Sheep numbers are similar to those in 1940 while goat numbers are substantially lower, but lack of data in between these dates prevents any analysis.

Discussion

Grazing and range degradation

To understand the full impact of grazing by livestock, the long-term history of grasslands must be considered. Grasslike pollen occured as early as the Eocene (50 million years ago; Ma), while pollen of other grassland components can be traced to the Miocene (23–5 Ma), but evidence for treeless prairies does not appear before about 11,000 years ago (Martin 1975b). The development of this biome, Paul S. Martin (1975a, b) has argued, was due to the disappearance of the great herbivores at the end of the Pleistocene. Several causes for these extinctions have been forwarded, but essentially they are climate-mediated vs. the human overkill model proposed by Martin (1973). We are convinced by Martin's hypothesis, but an analysis of the competing explanations is far beyond the scope of this contribution.

Data on Late Pleistocene fauna in our study region is limited, and only one site has been explored with some intensity: El Cedazo, near the city of Aguascalientes. This site has rendered fossils of several herbivores (taxonomically unrevised names): mastodon (Mammut americanus), Columbian mammoth (Mammuthus columbi, as M. cf. meriodionalis), eight species of horse (genera Equus, Hemionus and Hesperohippus), a peccary (Platygonus sp.), four camels (genera Camelops and Tanupolama), four pronghorns (genera Stockoceros, Tetrameryx and Capromeryx), deer (Odocoileus halli) and bison (Bison aguascalentensis), and a tortoise (Gopherus auffenbergi) (Mooser, 1972; Mooser and Dalquest, 1975). In addition to this site, there are fossils of mammoth (Mammuthus sp.) and mastodon from Villa Hidalgo, Zacatecas (Puga Pérez et al., 2011; Polaco et al., 1998) and of camel (Camelops hesternus), horse (Equus conversidens), bison (Bison bison) and Columbian mammoth from Laguna de las Cruces, San Luis Potosí, (Alvarez, 1982). Other paleontological sites relatively nearby (El Ocote, Gto. and San Juan de los Lagos, Jal.) are much older (late Miocene and Plio-Pleistocene, respectively).

Although there are no known Pleistocene megafauna kill sites or other evidence of Late Pleistocene hunting in the region, there is no reason why regional defaunation would have been caused by factors different from those in the rest of North America. Thus, the grasslands in the southern part of the Mexican Plateau that the Spaniards found upon their first arrival in the 16th Century can be assumed to have developed as a result of the human-caused Pleistocene defaunation, and considered evolution-arily anomalous, and therefore were highly susceptible to be transformed by grazing (Martin, 1975a, b).

After domestic herbivores were introduced to the region, three livestock periods can be defined clearly, as shown in **Figure 7**. From the mid-16th to the mid-17th Centuries, cattle was nearly the only domestic grazer; from the mid-17th to the late 19th Century, sheep dominated; and after this time, especially after the mid-20th, a mixture of sheep, goats, horses, asses, and few cattle grazed the range.

The first period began when Spanish cattlemen entered the region and found lush grasslands, claimed to have been tall enough to reach the belly of horses (Crosby, 1972). Considering this and the total rainfall in the region, the original vegetation could have been similar to a lush mixed grass prairie, lacking trees for the most part. Their specific composition is not known, but the Vaquerías cattle exclosure can be taken as a rough approximation. The upper panel of Figure 2, from inside this exclosure, shows the ground was covered almost completely (actually 99%) by herbaceous vegetation ~60 cm high. As in the exclusion, purple muhly and forbs could have been major components of such early-16th Century grasslands, surely along with other species that thrive in the absence of grazing, perhaps needle gramma (Bouteloua aristidoides), sideoats grass (B. curtipendula), Arizona cottontop (Digitaria californica) and Mexican lovegrass (Eragrostis mexicana) which currently occur in the region, but tolerate grazing poorly.

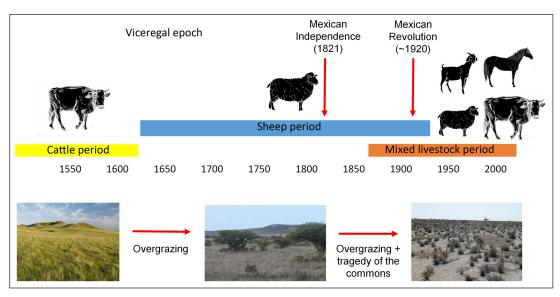


Figure 7: Livestock ranching on grasslands in the southern part of the Mexican Plateau. Three clear periods in livestock species are evidenced by historical data. These correspond to hypothesized changes in grassland characteristics caused by overgrazing. DOI: https://doi.org/10.1525/elementa.416.f7

This type of lush grassland encountered at the time was prime rangeland for cattle. In addition, cattle was the most convenient productive choice for early settlers as the area was under siege from the native inhabitants, and cattle requires less care and working hands to tend. Because of the sensitivity to grazing of the plants in these grasslands, and because grazing pressure during colonial times was very high, the community started to change. High grazing pressure is inferred from the available data. For example, in 1582, an area north of San Juan del Río measuring 9 square leagues (15 800 ha) was reportedly being grazed by >100 000 cattle, 200 000 sheep, and 10 000 mares (Vargas in Morrisey, 1951). This amounts to roughly 125 000 Animal Units (AU; 1 AU is defined by a 445 Kg cow with or without an unweaned calf, or an ecological equivalent). Current open medium grasslands in that area when in good condition have a recommended stocking rate of 6.62 ha/AU (Diario Oficial de la Federación, 23 June 1982); so the referred area would safely support 2375 AU. Thus, even if the reported numbers were a gross overestimate, grazing would have greatly exceeded the carrying capacity of the area. Likewise, throughout the surroundings of the current cities of Durango and Nombre de Dios, Durango, cattle "covered the land" less than 30 years after the Spaniards arrived (Morrisey, 1951) suggesting that these areas were also greatly overstocked.

In the Llanos de Ojuelos, the 8700 calves branded at El Tecuán in 1629 and 1630 would mean about 6250 cows (assuming a 70% yearly pregnancy rate) plus about 1100 A.U. in horses (1 mature horse = 1.25 AU), all on 1756 ha. The recommended stocking rate of grasslands on the plains and hills of southern San Luis Potosí in good condition is 9.65 ha/AU, thus the amount of live-stock calculated would require more than 70 000 ha to graze without causing serious impacts; this is 40 times the size of the ranch. Even if ecological carrying capacity at that time was somewhat higher, and cattle were grazed

elsewhere as well, the range seems to have been severely abused.

Despite the spatial and chronological patchiness of the data, it is reasonable to suppose that such high stocking rates were widespread, and some observations in historical documents support this. In 1585, the grasslands of the highlands of Jalisco were allegedly wasted by cattle grazing "...without measure..." (AGI/Audiencia de Guadalajara 6: "Licenciado Pinedo al Rey, 30 de marzo de 1585"), while in 1640 the Zacatecas rangelands had "...la circunstancia importantísima del agotamiento de los pastos" ("... the very important circumstance of the exhaustion of the grasses"; Esparza Sánchez, 1988), which might be interpreted as to reflect overgrazing. Likewise, in the early or mid-17th Century, cattle sent from Lagos to be fattened in Ojuelos were complained of as being lean and weak (Calvo, 1989), which, as no cause was indicated, might suggest deterioration of the range where they had been foraging.

Thus, by the early decades of the 17th Century, grasslands had deteriorated, passing from tall and dense grass-herb communities to short grasslands. These would have been composed of species that were more grazing-resistant, by having evolved under grazing. They were not reported precisely, but we can hypothesize about them. Considering the regional grass diversity we believe it is safe to presume that gramma grasses, especially the blue gramma (*B. gracilis*) and the Mexican plateau gramma (*B. scorpioides*), were major components of these short-grass grasslands, perhaps including common wolfstail (*Lycurus phleoides*) and other grazing-tolerant (to some level) plants. Some soil erosion could have developed by this time.

The change in the type of rangeland in the early 17th Century, we contend, was the major cause of a shift in the livestock species raised that defined the second livestock period in the region: that of sheep ranching. Onset of sheep ranching in the Llanos de Ojuelos and surrounding valleys was much later than in nearby regions, some of which were more suitable for sheep than for cattle from

the beginning. For example, mountains to the southeast had xeric shrublands, and the Colotlán area had shrublands and forests, while the areas around San Luis Potosí were drier and can be suspected to have lacked the lush pre-Contact grasslands of the Llanos de Ojuelos. It could be argued that sheep raising had not been taken up in the area due to the Chichimeca War, but when this conflict ended, the Llanos de Ojuelos did remained cattle country for more than two decades.

Some writers (Chevalier, 1963; Esparza Sánchez, 1988) have argued that the change from cattle to sheep in the southern section of the Mexican Plateau in the mid-17th Century resulted from the establishment of the hacienda system. Certainly, the hacienda system and sheep raising work well together, and both were the trademarks of the region by the late 19th century. However, in the Llanos de Ojuelos the hacienda system was strongly rooted long before sheep grazing began, and already existed when sheep were stocked heavily in other areas of the southern Mexican Plateau (Florescano, 1990). Also, after the Chichimeca War ended, availability of ranch hands to serve as sheep herders would not have been a limitation for sheep raising. So, arguing that sheep raising depended on development of the local hacienda system seems untenable. Rather, we concur with Jordan (1993) who, referring to the southern part of El Bajío area, indicated "[t]he dwindling cattle herds and the simultaneous rapid rise of sheep raising presented the most obvious clue that range damage had occurred." The earliest widespread impact to the native vegetation in the Llanos de Ojuelos was caused by cattle, and it was this impact on the grasslands, and the transition from tall to short grasses, we contend, that drove the change from cattle to sheep during the 17th century.

When cattle was substituted by sheep, grazing pressure did not seem to ease. The figures of 50,000 and 40,000 sheep in 1664 at the haciendas of Santiago de las Chinampas and de la Misericordia, each measuring 1 allotment for large stock (Gómez Serrano and Delgado Aguilar, 2005) seems overly exaggerated, but suggest severe overstocking. At the Mayorazgo de Rincón Gallardo, in 1697, the situation is more difficult to establish. In addition to 255 caballerías (10,950 ha of farmland), it included 183 allotments for large stock (321,348 ha) and 19 for small stock (14,820 ha), and reportedly sustained 100 000 sheep, and few other livestock (Chevalier, 1963). One AU equals 3.3 ewe + lamb, or 5 mature sheep; thus, at 9.65 ha/AU about 2.4 ha are required for each sheep. If, as required by law, only small-stock allotments were used for sheep grazing, the optimal carrying capacity (6143 sheep) was greatly exceeded. If ranchers went against the law, which is likely at least partially, and both large and small stock allotments were used to graze the sheep, the size of the herd would have been lower than the current carrying capacity recommendations of 34,836 AU (Alcaide Aguilar, 2004). Even if numbers were underreported somewhat (Serrera Contreras, 1974), in the latter case the range might have not been overstocked at that time. But the real condition cannot be known.

During 1780–1795, a general deficit of cattle provisioning from the north, including our region, to México City was attributed to the scarcity or lack of grasslands, droughts, overharvesting of females, livestock change, and even the expulsion of the Jesuits from the country (Serrera Contreras, 2015). Interestingly, grassland degradation was not given as a potential explanation, although "scarcity of grasslands" might point at it. Two other indirect pieces of information suggest overgrazing in the region. First, in 1827, Henry George Ward (1828) found jackrabbits to be abundant on the plains of San Felipe. Jackrabbits are not abundant in grasslands in good condition but thrive in overgrazed ones and shrublands (Loft et al., 1987; Fogden, 1978). Second, by the end of the 19th Century (1891–1893) the consumption of toxic plants, including alfombrilla (Drymaria arenaroides, which contains alcaloids, oxalates and saponins) and toloache (jimsonweed, Datura stramonium, which contains tropane alkaloids, atropine, hyscyamine, and scopolamine) was becoming one of the leading causes of livestock death (Esparza Sánchez, 1988). In the region, these plants are usually encouraged by overgrazing.

In agreement with the former, at the end of the 19th Century, the increase in goat numbers in Ojuelos points at the beginning of another shift, this time from shortgrasses to ranges with cespitose grasses and shrubs. Such a shift seems supported by a 1940s report of the grasslands in the Zacatecas part of Los Llanos as having much "zacate chino" (possibly the cespitose buffalo grass, B. dactyloides, currently known in the region as "zacate borreguero", "sheepgrass"), which results from overgrazing (Hernández Xolocotzi, 1964; Miranda and Hernández Xolocotzi, 1964), along with much gatuño (Mimosa sp., catlcaw), engordacabra (Dalea bicolor; silver dalea), and vara dulce (Eysenhardtia polystachya; Mexican kidneywood) (de la Peña, 1948), all shrubs, in the region, typical of advanced overgrazing. Jimmyweed and some other grazing-resistant grasses (B. dactyloides, B. repens, Scleropogon brevifolius, Sporobolus spp., Hilaria cenchroides, H. mutica) were likely also present at this time. Soil erosion was likely severe in some parts. Such a change in the composition and plant cover of the range made monocultural sheep production unprofitable. Thus, the third period, one of mixed and smaller herds of different livestock species, began in the second part of the 19th Century.

The Mexican Revolution (1910–1920) was a major disruption in much of the country, but locally there seem to have been no major impacts, and sheep raising was not interrupted. After the revolt ended an increased peasant population tried to solve their needs partially trough placing additional livestock on the range, which contributed to exacerbate its deterioration. By the mid-20th century many of the rangelands supported only cespitose grass remnants, and barely so, accompanied by invader plants like jimmyweed, locoweed (Astragalus mollisimus), and several shrubby legumes. Goat husbandry became important, along with the small-scale ranching of all other livestock species. The mixed herds currently present on many communal (ejido) rangelands, involving species with different foraging characteristics (Larson et al., 2015), are a practical response to the transformation of the former grasslands into low-productivity, but more heterogeneous, rangelands (Anderson, 2003).

The whole-state stocking rate in Zacatecas in 1940 was of 5.2 cattle heads, 4.7 horses, and 12.1 sheep and goats per km² (de la Peña, 1948). As these are state averages, they can be compared only very roughly with the livestock pressure upon the range in the Llanos de Ojuelos. These data represent 3.24 ha/AU, a stocking rate nearly three times higher than the recommended 8.9 ha/AU for grasslands in "good condition" in our area. Not surprisingly, an increase in undesirable (for livestock) plants and severe erosion in grasslands in Villa de Arriaga was blamed on overgrazing, combined with the dispersion of nopal by cattle (Gómez González, 1963).

There is no record on the frequency, or even the existence, of grassland fires under pre-Spanish conditions. If fires did exist, which is likely, they were eliminated as the grassland degraded from the mixed grassland to short and, later, cespitose. We can only speculate that lack of wildfires under these conditions favored further the appearance of shrubs (*sensu* Leopold, 1924; Archer, 1989; Archer et al., 2017).

Effects on wildlife

The impact of grazing-induced habitat changes on wildlife in the southern portion of the Mexican Plateau is difficult to identify precisely, as the species in the original grasslands were not recorded. Thus, analyzing changes in wildlife during the last 500 years requires speculation based on current natural history knowledge. For example, the American pronghorn (Antilocapra americana) was distributed originally on grasslands as far South as the current Mexican states of Hidalgo and Estado de México (Leopold 1959). Although there is no mention of pronghorn in our region in historical documents and it is not included in Hall's (1981) distribution map, there is archaeological evidence of its presence in nearby Villa de Reyes. This species would have certainly occurred in the Llanos de Ojuelos grasslands as there are not geographical barriers between this area and Villa de Reyes. Pronghorns would have been strongly impacted by overgrazing, perhaps even long before the cattle period ended. They could have survived in small mixed grass remnants, but as a 1970s reintroduction in San Luis Potosí showed (Mellink et al., 1986; EM pers. obs.), they would have been eventually extirpated by coyotes (Canis latrans) and, perhaps, by wolves (C. lupus) depredating them.

Similar, but even less known, are tortoises. The Bolson tortoise (*Gopherus flavomarginatus*), currently restricted to a small area 400 km north of our study region, was widespread at the end of the Pleistocene, being present in much of central Mexico (Auffenberg in Ureña-Aranda et al., 2015), including a fossil described from Aguascalientes (named *G. auffenbergi*; Mooser, 1972). Whether this species survived until the arrival of the Spaniards in the region is not known, but given that arid and semiarid grasslands are a prime habitat for it, it is not unlikely. Quality of Bolson tortoise habitat is a direct function of vegetation cover (Becerra López et al., 2017), so overgrazing would have impacted the species to its extirpation.

There are species in the region whose optimum known habitat is that of dense grass/herb vegetation. In the region they currently persist in small, sometimes ephemeral patches of this type, and their abundance increases or seems to increase after a good rainy season promotes the growth of tall herbaceous and grassy annuals. One of such species that we can expect to have been abundant in pre-Contact grasslands is the pocket gopher (Thomomys umbrinus). The deep, well-drained pre-Contact soils, with abundant herbaceous vegetation would have been prime habitat for it. Along with it would be its burrow associates, including the Plateau Tiger Salamander (Ambystoma velasci), southern spadefoot (Spea multiplicata) and Mexican bull snake (Pituophis deppei). Also, the western harvest mouse (Reithrodontomys megalotis) prefers the habitat provided by thick herbaceous vegetation, and was surely also abundant in the early 16th Century grasslands. Another rodent candidate of pre-Contact grasslands is the Mexican vole (Microtus mexicanus). It has not been recorded currently in the region, but the area is within the species' general distribution (Hall 1981), and the lush grasslands would have provided adequate habitat for it.

Two species of birds, surely among others, that were also abundant when the Spaniards arrived and were much reduced by grazing by livestock were meadowlarks (mostly the eastern meadowlark, *Sturnella magna*), and the Mexican duck (*Anas platyrhynchos diazi*). The latter species currently nests sparsely in the region's grasslands due to the lack of proper nesting cover (Mellink, 1994). Its abundance has increased in El Llano allegedly as a result of the conversion of maize fields to alfalfa agriculture, which provides better nesting habitat (Mellink et al., 2018a).

When the grasslands changed from mixed to low not only were some species impacted negatively, but several other species of wildlife can be hypothesized to have been benefited. These include white-sided jackrabbit (*Lepus callotis*), Ord's kangaroo rat (*Dipodomys ordii*), Chihuahuan grasshopper mouse (*Onychomys arenicola*), scaled quail (*Callipepla squamata*), bobwhite quail (*Colinus virginianus*), horned lark (*Eremophila alpestris*), speckled earless lizard (*Holbrookia approximans*), bunch grass lizard (*Sceloporus scalaris*), mountain horned lizard (*Phrynosoma orbiculare*), large-nosed earthsnake (*Conopsis nasus*), and rattlesnakes (*Crotalus spp.*), which prefer short, moderately open grasslands or have a larger prey base in them.

As conditions deteriorated further, many of the species that increased in the shortgrass sheep grazing period saw their numbers reduced or their populations constrained to small remnant patches or habitat substitutes. For example, the two quail species in the area (scaled and bobwhite), which are absent from many grasslands as a result of their extreme deteriorated condition currently find habitat mostly in nopal orchards (Mellink et al., 2016). The white-sided jackrabbit was substituted by the black-tailed jackrabbit (*L. californicus*) which contrary to the shortgrass preference of the prior prefers shrublands (Dunn et al., 1982), while Ord's kangaroo rat was substituted by the ornate kangaroo rat (*D. ornatus*) which uses more open and shrubby habitats (Riojas-López et al., 2018).

Other changes in this transition to more open, shrubby vegetation are more difficult to deduce, as they vary as a function of the specific characteristics of the transformed habitat. For example, in semiarid grasslands in western San Luis Potosí the impact of grazing on lizards, birds, and rodents and lagomorphs depended respectively on how it modified the horizontal heterogeneity of the habitat (Valenzuela Pérez, 1987), the vertical heterogeneity (Mellink and Valenzuela, 1992), and vegetation cover and composition (Mellink and Valenzuela, 1995).

Concluding remarks

Landscape changes in other arid and semiarid regions in Mexico indicate that the introduction of settler non-indigenous livestock was an ecological turning point. This was documented thoroughly in the Valle de Malpaso, some 130 km northwest of our study region, in which Elliott et al. (2010) concluded that "[t]he most dramatic changes detected in the valley resulted from the erosion associated with Spanish Colonial grazing and deforestation that began in the 16th century." Likewise, grazing by sheep was a major driver of severe environmental degradation in the Valle del Mezquital in central Mexico (Melville, 1994). The Spaniards that arrived at Malpaso shared a common style of livestock husbandry with those reaching other arid and semiarid regions of northern Mexico, and the severe impacts on the landscape due to overgrazing and deforestation elsewhere, including the Llanos de Ojuelos and its surroundings, likely mirrored those at Malpaso.

In the Llanos de Ojuelos, the ecological effects of overgrazing include changes in vegetation, as exhibited by plant composition within and outside the livestock exclosure near Vaquerías and in ranches in better and worst condition. The evident impacts, however, go much further than vegetation and include the development of erosive pedestals and gullies, exemplified in Figure 8, which are abundant throughout the region. These can be safely assumed to have resulted from heavy grazing, as has been documented in the state of Zacatecas (López Reyes, 2001; Echavarría Chairez et al., 2007b) and in other parts of the world (Rauzi and Hanson, 1966; Mwendera and Mohamed Saleem, 1997; Scurlock, 1998; Sharrow, 2007). As a result of the change in cover and soil compaction, in agreement with findings in other places, it can be assumed that soil temperature, moisture, organic matter, nitrogen, and capacity to store carbon have been altered (Balling et al., 1998; Abril and Bucher, 1999; Conant and Paustian, 2002), as have been the populations of several wildlife species. These profound changes in the region have impacted not only the capacity to support ranching and conserve wildlife and other ecosystem services: They have also been the major driver of changes in the dominant livestock through time.

Some of the current ranges are in extremely poor condition for livestock production and for biodiversity conservation, and its improvement would benefit both. We concur with Brown and McDonald (1995) that it is unpractical and nonsensical to revert grasslands to their pre-Hispanic condition and that we must find ways to maintain openspace ecosystems under human management schemes. After all, the model of a rangeland in good condition is that of an "artificial" system, devoid of large herbivores (*sensu* Martin, 1975a). So, the research efforts devoted to keep grass communities and eradicate certain species



Figure 8: Large gully developed as a result of overgrazing near Vaquerías, Jalisco (photograph: Eric Mellink, February 2017). Several gullies of this magnitude exist in the area. Even worse is that the area outside the gully is already severely eroded. The bottom of the gully is exposed duripan. Some areas in the region are so severely eroded that only duripan is left. DOI: https://doi.org/10.1525/elementa.416.f8

whose seeds are favored by their passage through the guts of cattle, seem out of evolutionary place. The dissemination of mesquite and other plants just reestablishes lost ecological processes (Martin, 1975b; Janzen and Martin, 1982). We cannot discard the hypothesis that the system has been pushed beyond a transitional threshold into a new stable state from which it would be very difficult to return (*sensu* Archer, 1989). Thus, rather than seeking to match idyllic versions of the grasslands encountered by the Spaniards in the 16th Century, contemporary grassland management and research efforts in the Llanos de Ojuelos should be directed at combining socioeconomic needs with specific biodiversity and soil conservation targets.

The Vaquerías livestock exclosure suggests that many of the grasslands in the area can recover lush herbaceous communities if grazing pressure is taken away. However, any scheme that focuses on range improvement must be accepted by ranchers, and this implies that livestock cannot be removed altogether, but this is not necessary. As Jordan (1993) indicated, "[t]he ecological problem of ranching... is not grazing, but specialized overgrazing".

The possibility of improving grassland condition without eliminating completely livestock is evidenced by two cases in which the range has improved substantially after easing, but not eliminating, grazing. No data on vegetation cover and composition before and after the easing of grazing in these two cases are available, but the improvements have been visually evident. The first case is that of a range experimental station near Vaguerías that was established in 1979, after which grazing was adjusted to technical recommendations. This particular site had an open shortgrass grassland in fairly good condition (EM pers. obs.), and now supports a dense and tall herbaceous habitat. The second case is that of rangeland that was dedicated to raise beef cattle, and which was in very poor condition as the result of heavy grazing (F. Santoyo, current owner, pers. com.). Since changing ownership in 2001 the range has been devoted to the rearing of fighting bulls. This breed is stocked at much lower densities than beef cattle and, as a result, the rangeland has improved.

To improve the condition of the grasslands without removing grazing, rotational grazing offers the most appealing management strategy (Echavarría Chaírez et al., 2007a; Krausman et al., 2009). Several variants exist, but at its core it involves dividing the range into subunits and moving the animals between them. Any single subunit is grazed for a small amount of time and then allowed to recover from grazing for a longer time. In some cases, a subunit can rest for over a year. Thus, the plants foraged upon are allowed to recover and deepen their root systems. Also, under the more intensive grazing, livestock eat not only the most palatable plants, but also the other, less preferred ones, as opposed to continuous grazing where grazing can be highly selective, lowering the competition ability of the prior and allowing the increase of latter.

One drawback of rotational grazing is that it requires a heavy investment in fences and increased labor to manage the livestock. This is however a one-time investment (with later maintenance) which pays off with time, as improved grasslands allow for increases in the stock. A point of hope is that currently subsidy programs involving rotational grazing are beginning to be implemented in the region by the Mexican government. However, these are focused solely on the livestock part of the system and neglect the wildlife component, which has resulted in fences that may interfere with the movement of wildlife. This should be adjusted.

A complementary approach to that of rotational grazing is that of "targeted grazing" (Launchbaugh and Walker, 2006). In it, a specific outcome, i.e. desired plant community, must be pictured, and grazing efforts directed to that end. Much knowledge is needed to tailor targeted grazing management finely, but some broad approaches could help in the restoration of regional grasslands. For severely overgrazed grasslands in the southern Chihuahuan Desert, stoloniferous, clonal grasses have been suggested for the initiation of recovery efforts, while bunch grasses would be those of a second phase (Yeaton and Flores Flores 2009). For our study region, buffalo grass and the central Mexico tobosa grass (Hilaria cenchroides) seem convenient species for targeted grazing on the most degraded grasslands, while the blue and Mexican plateau grammas are suitable targets for less degraded ones. With time, the managed grasslands would recover to taller and denser herbaceous communities.

Lastly, the Vaquerías livestock exclosure has proven its value in understanding some of the changes in the region's grasslands brought about by grazing (Aguado-Santacruz and García-Moya, 1998; Aguado-Santacruz et al., 2000; Riojas-López and Mellink, 2005; Almanzor-Rojas and MER-L, unpub. data). Maintaining this exclosure, and establishing others in other areas can be instrumental to understand the composition and ecological processes of regional grasslands. This would help to refine grassland management strategies according to specific biological conservation and production needs.

Although we focus on a specific region, the picture provided is a potential framework for interpreting livestockmediated grassland deterioration in other semiarid areas throughout the world. From our review and analysis we conclude that:

- Grazing in the Llanos de Ojuelos can be divided in three periods: cattle production from the mid-16th to the mid-17th Century, followed by the substitution of cattle by sheep as a response to the change from tall to short grasses, until serious grassland degradation by the mid-20th Century caused a shift to goats and horses, along with sheep, asses and some cattle.
- 2) Grazing by livestock has gradually impacted grassland structure and productivity in the Llanos de Ojuelos and nearby areas, curtailing their capacity to provide environmental services in the form of water retention, habitat for wildlife and forage for livestock production. Also, we hypothesized that as a result at least 20 native vertebrate species have probably been negatively affected, while some other species have profited.
- 3) Grassland improvement is still possible in many ranges in the area, and should be carried out, but re-

Art. 20, page 15 of 20

alistic objectives based on biodiversity conservation and livestock production should be considered, rather than a utopic version of pre-livestock times. Grassland restoration in many cases would not require the removal of all cattle, as rotational grazing, along with a target grazing approach focused on grazing-resistant native grass species, can be used to this end.

4) Maintaining the currently existing livestock exclosure and establishing new ones throughout the region would be very valuable for the understanding of the ecological processes involved in grazing, and would be an aid to the conservation of some of the animal species impacted negatively by overgrazing.

Data Accessibility Statement

We confirm that both authors, Eric Mellink and Mónica E. Riojas-López have no Data Accessibility Statements.

Supplemental file

The supplemental file for this article can be found as follows:

 Mellink and Riojas-López – Supplemental material. Location of all places indicated in the text. An alphanumeric listing indicates, with letters, extra-regional sites indicated on a small-scale insert map, and, with numbers, all sites in the region, in semi clock-wise arrangement. A second listing indicates all locations alphabetically, indicating their placing letter, in the small insert map, or number, in the large main map. DOI: https://doi.org/10.1525/elementa.416.s1

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Competing interests

The authors have no competing interests to declare.

Author contributions

- · Contributed to conception and design: EM, MER-L
- · Contributed to acquisition of data: EM, MER-L
- Contributed to analysis and interpretation of data: EM, MER-L
- · Drafted and/or revised the article: EM, MER-L
- Approved the submitted version for publication: EM, MER-L

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Art. 20, page 19 of 20

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