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Restoration sites on the Californian coast have different ecological histories that can influence restoration success

Élise BUISSON¹, Thierry DUTOIT¹

1. IMBE – Institut méditerranéen de biodiversité et d'Écologie, Avignon Université, CNRS, IRD, Aix Marseille Université. IUT d'Avignon, Agroparc BP 61207, 84911 Avignon cedex 9, France

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Abstract

For each restoration project, it is essential to define a reference ecosystem towards which ecological restoration aims. Historical information may be useful in the construction of the reference model and in finding out about the type and degree of disturbances that have caused degradation on the site, as legacies of past human land-uses have been shown to be major determinants of vegetation and plant diversity even in the very long term. The aim of this paper is to retrace the history of three sites where restoration protocols were tested, to better apprehend the potential reference ecosystems as well as the disturbances that degraded them. To do so, we first compiled information on the reference ecosystems at the landscape scale. Then, we compiled historical and agricultural information at the scale of the sites from local historical documents, historical reviews and aerial photographs. The three sites most likely were grasslands or oak savannas before European settlement. Grasslands used to cover 8.9 million ha in California. They were species-rich grasslands managed with fire by the native people and grazed by native ungulates. Early settlers introduced cattle grazing and changed fire regimes. Later on, many grasslands were converted to

cultivation. All three sites were used for ranching and sometimes overgrazed. At least two of them were cultivated, probably leading to restoration being harder there, as plowing eliminates perennial species, destroys the seedbank, changes soil characteristics.

Introduction

Ecological restoration and historical ecology

Ecological restoration as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (Gann *et al.*, 2019). For each restoration project, it is essential to define the goals towards which ecological restoration aims in order to plan adequate restoration activities, monitor progress and assess success (Holl & Cairns Jr., 2002; Gann *et al.*, 2019). The reference model describes the expected condition that the restoration site would have been in if it had not been degraded. This model is not the historic condition, but rather reflects predicted changes in environmental conditions

Keywords: *Danthonia californica*, fire, grasslands, grassy biome, grazing, *Nassella pulchra*, oak savanna, prairie, *Stipa pulchra*.

(Gann *et al.*, 2019). It can help define the reference ecosystem that is the target of ecological restoration.

Historical information may be useful in the construction of the reference model and in finding out about the type and degree of disturbances that have caused degradation on the site (Gann *et al.*, 2019) because it is now well known that present ecological factors and functional relationships alone cannot explain present-day vegetation composition and dynamics (Purschke *et al.*, 2012). In its Primer, the Society for Ecological Restoration advises gathering of essential baseline data on the reference ecosystem, including the abiotic environment and important aspects of biodiversity, normal periodic stress events and traditional cultural practices (SER - Society for Ecological Restoration International Science & Policy Working Groups, 2004). Not only does the reference ecosystem need to be described, but the disturbances that degraded the site also have to be identified.

Legacies of human land-uses and historical ecology

Legacies of past human land-uses have been shown to be major determinants of vegetation and plant diversity in numerous ecosystems other the world (Dambrine *et al.*, 2007; Karlík & Poschlod, 2014; Levis *et al.*, 2017; Maezumi *et al.*, 2018a, b). Understanding how land-use legacies influence present day ecosystem composition and function is the aim of historical ecology a sub-discipline of ecological science. It has been defined as the field of ecology that reconstructs the history of ecosystems and landscapes to analyze impacts on biodiversity and ecosystem function (Southgate-Russell, 2019). It of course includes causes and consequences of the interactions between man and the environment (Beller *et al.*, 2017). Understanding present-day plant communities also implies putting them in their historical context.

Understanding drivers of past vegetation changes also allows predicting future changes in response to interacting environmental and human drivers (Crumley, 2018). In a context of global changes, it is increasingly important to evaluate how long human impacts might last (Southgate-Russell, 2019). It is therefore essential to determine whether long-term impacts follow similar patterns across ecosystems in the world and to identify

underlying processes for a more functional historical ecology approach.

Until now, land-use legacies have been most thoroughly identified in temperate forest plant communities (Brunet *et al.*, 2000; Bossuyt *et al.*, 2002; Graae *et al.*, 2003) and dating back from the Roman period (Dupouey *et al.*, 2002; Vanwallegem *et al.*, 2004; Dambrine *et al.*, 2007; Plue *et al.*, 2008). Similar time scales and processes have been identified in herbaceous ecosystems even if they were subjected to frequent grazing and fire along their history (Pärtel *et al.*, 2007; Saatkamp *et al.*, 2021).

Grasslands in California

Grasslands cover about 40% of the Earth (Dixon *et al.*, 2014) and provide numerous ecosystem services, such as food production, water supply and regulation, carbon storage, and cultural services (Bardgett *et al.*, 2021). In California, grasslands may have covered 8.9 million hectares, of which only about 800,000 hectares remain (Noss & Peters, 1995; Stromberg & Kephart, 1996). They are the eighth rarest ecosystem in the United States (Santa Cruz County CNPS, 2022). They range from open grasslands to oak savannas and herbaceous patches within the chaparral (Heady *et al.*, 1988), and are classified in four main types: north coastal grasslands, valley and south coastal grasslands, cold desert grasslands and warm desert grasslands (Keeler-Wolf *et al.*, 2007). Northern coastal grasslands, also called Californian coastal prairies, *Festuca-Danthonia* grasslands or coastal terrace prairies, extend along the coast, within the area influenced by coastal fog, from southern Oregon to the Channel Islands (Heady *et al.*, 1988; Ford & Hayes, 2007; Keeler-Wolf *et al.*, 2007) (Figure 1).

In some areas of Santa Cruz County, California, prairie habitats support native bunchgrasses and as many as 250 species of native wildflowers (e.g. *Holocarpha macradenia* (Santa Cruz Tarplant) and *Plagiobothrys chorisianus* (artist's popcorn flower)), 13 of which are listed in the Inventory of Rare and Endangered Plants of California (1995) (Santa Cruz County CNPS, 2022)(CNPS, 2005). Plant diversity supports a great diversity of insect species, such as *Schinia* sp. (diurnal noctuid moths), *Cicindela ohlone* (Ohlone Tiger Beetle) and *Adela oplerella* (Opler's long horned moth) (CNPS, 2005).

The major threats to coastal prairies include urban and agricultural development, shrub encroachment, intensive livestock grazing, exotic plant invasions and fire suppression (Comer *et al.*, 2022).

Objectives

While the conservation and management of the remaining grasslands is the highest priority, restoration of degraded grasslands has been implemented at many sites (Stromberg *et al.*, 2007). Between 2001 and 2005, we carried out restoration experiments at three sites along the coast of California: on Stanford University campus (Santa Clara County), on the University of California Santa Cruz UCSC campus (Santa Cruz County) and on Porter Ranch, near Elkhorn Slough (Monterey County) (Figure 1). The experiments aimed at re-introducing two native perennial bunchgrasses. The Stanford site, was planted with *Stipa pulchra*. This site is located in the Stanford foothills, less than 30km from the coast, on a gentle hill facing east, and had two dominant vegetation types: annual exotic grasses or exotic forbs such as *Brassica nigra* (Buisson *et al.*, 2008). Two sites other were planted with *Danthonia californica*. The UCSC and the Elkhorn sites are located less than 7km from the coast, have similar slopes (<10% facing south) and soils (sandy loam soil > 1m deep) and were dominated by annual European grasses (Buisson *et al.*, 2006). The aim of this paper is (1) to retrace the history of these sites within their landscape, (2) to better apprehend the potential reference ecosystems as well as the disturbances that degraded them and (3) to discuss the potential influence of the different former land uses on present restoration success.

Methods

SER proposes to use as many sources of information as possible to describe the reference ecosystem: ecological descriptions, species lists, data on the physical conditions, aerial and ground-level photographs, and paleoecological evidence and historical accounts (SER - Society for Ecological Restoration International Science & Policy Working Groups, 2004). To re-trace historical trajectories more particularly, various sources of information are used, such as documentary



Figure 1 – Distribution of California coastal prairies (grey areas) (Ford & Hayes 2007) and location of the three study sites in the San Francisco Bay – Monterey Bay area.

archives (maps, land surveys), photographs, diaries, interviews with local farmers, old vegetation records (Wells *et al.*, 1976; Sheail, 1980; Rackham, 2000; Egan *et al.*, 2005; Southgate-Russell, 2019). Information compiled from these sources although varied is often limited in quantity and quality (Swetnam *et al.*, 1999). Here, we first compiled information on the reference ecosystems at the landscape scale. Then, we compiled historical and agricultural information at the scale of the sites (e.g. cultivation dates, time since abandonment, cultivation practices, crops, and other disturbances – Table 1) from local historical documents, historical reviews and aerial photographs.

Table 1 – Yields, in metric tons, of cereals (wheat, barley, corn) and legumes (bean, lentils, garbanzo beans and peas) and number of bred animals in Mission Santa Cruz in the early days (1791), at production peaks and around its end (1834) (Martin, 1879).

Year	Cereals	Legumes	Cattle	Sheep-Goats	Pigs	Horses-Mules
1792	62.1	3.3	130	146	0	4
1806			2,400	5,400	130	3,396
1818	705.0	255.0				
1821	637.5	41.8				
1827			3,600	8,000	0	902
1832	115.5	42.3	3,600	5,211	0	425

Before European settlement

The distribution and composition of Californian grasslands before European settlement remain uncertain. Until recently, the pre-settlement landscape in California was believed to be largely dominated by grasslands. *Stipa pulchra*, a perennial bunchgrass first described by Fremont (1848 in Holstein, 2001) in 1845 in the Sierra Nevada foothills and in the inner Coastal Ranges, was believed to be the original bunchgrass dominating these grasslands (Clements, 1920 in Clements *et al.*, 1929), even the grasslands now dominated by annual exotics.

The landscape was however not so homogeneously dominated by *Stipa pulchra* grasslands as previously thought (Bartolome *et al.*, 1986). The potential natural vegetation of most grasslands would be some type of woody community as there are no edaphic or climatic constraints limiting woody species development (Gordon, 1977). However, grasslands were well-represented ecosystems in the state because native ungulates, such as pronghorn antelopes (*Antilocapra americana*), mule deer (*Odocoileus hemionus*) and bison (*Bison bison*) had been grazing the area for more than 15,000 years (Edwards, 1996) and Native Americans extensively managed their landscape with fire (Keeley, 2002). On the land extending from the San Francisco Bay Area to beyond the Monterey Bay and inland to Mount Hamilton Range, the Ohlone people lived and burnt grasslands in autumn to encourage new growth and to attract game (Margolin, 1997). Both the Ohlone people and native ungulates maintained large areas of species-rich grasslands, as sometimes still observed on serpentine outcrops (Huenneke *et al.*, 1990; Harrison *et al.*, 2001).

However, not all actual grasslands were grasslands before European settlement. Depending on authors, Central Valley grasslands may have been 1) broad sclerophyll forests, chaparral and/or annual grasslands (Hamilton, 1997); 2) marshlands, riparian woodlands (Heady *et al.*, 1988); 3) *Leymus triticoides*-dominated grasslands where rainfall was > 250mm/year, or; 4) annual forb-dominated grasslands where rainfall was < 250mm/year (Holstein, 2001). Actual Coastal Prairies may have been 1) coastal sage scrub, chaparral, oak woodlands, oak savannas and/or prairies (Hamilton, 1997); 2) *Stipa pulchra* grasslands in the Coastal Range with coarse sandy

soils, steep slopes and relatively low fertility (Holstein, 2001). The only way to differentiate these various options may be through the study of opal phytoliths (microscopic particles occurring in plants and persisting in the soil; (Bartolome *et al.*, 1986). Regardless, it is likely that the original coastal prairies had a greater cover of perennial bunchgrasses: *Danthonia californica* (California oatgrass), *Festuca rubra* (red fescue) or *Deschampsia cespitosa* (California hairgrass) were most probably found on the coast and *Stipa pulchra* (purple needlegrass) was more common in coastal prairies further inland (Heady, 1956). Although, the original area covered by grasslands is not known and their plant composition uncertain, grasslands were definitely part of the Californian landscape. As noted previously, California grasslands may have covered 8.9 million ha, of which about 1% remains (Noss & Peters, 1995; Stromberg & Kephart, 1996). Grasslands and prairies have evolved under moderate grazing pressure from native ungulates and burning management from native people, as well as periodic drought stress and burrowing mammals (Heady *et al.*, 1988).

Coastal Prairies after European settlement

The successive occupants of California had a different impact on the land. Exploration of California by European started as early as the mid-16th century and California became a colony of the Spanish empire in 1769. The impact of the Spanish on the land was first relatively moderate and started on the coast with the settlement of Missions and Presidios (military forts) from San Diego to San Francisco. The first cities were founded in 1777 (San José), 1781 (Los Angeles) and 1797 (Villa Branciforte) (California Historical Society, 2022). During that period, Native American burning of grasslands remained widespread (Gordon, 1977). Livestock supported most of the Spanish colony economy: ranchers used established grasslands as pastures and burned the woody community on the lowlands and on the lower slopes to create more pastures where cattle roamed freely (Gordon, 1977). Tillage and irrigation were minor activities and were limited to around the Missions. In 1821, Mexico gained its independence from Spain, California became

Mexican, and huge ranches developed. Burning was forbidden as it was negatively viewed by ranchers, but it was later reintroduced to clear more chaparral into pastures and to improve pastures and ensure maximum forage by sowing with oat and barley. Fires were suppressed again later (Dashe, 1982). After the 1846-1848 Mexican-American war, California became part of the United States. Around 1870, Americans started large-scale commercial agriculture, involving plowing, drainage and irrigation (Gordon, 1977).

Most of the Pajaro valley, Watsonville, and the coast of Santa Cruz county have been developed in agriculture and development (Santa Cruz County CNPS, 2022). Cattle and deer populations as well as fire maintain remaining grasslands, mainly composed of exotic species. The ground squirrel (*Otospermophilus beecheyi*), a native mammal that naturally lives in grasslands and oak savannas, thrived as pastures, grains and other crops increased. At some point, its populations increased to the point of being considered a pest, especially since the populations of their predators had decreased (Gordon, 1977; Luckenbach, 1982). More recent works show its role as an ecosystem engineer, supporting the food web through its burrowing activity, and the need for a better management for this species (Lenihan, 2007; McCullough Hennessy *et al.*, 2016)

The impacts of the post-European settlement disturbances and recovery have been well studied along the California coast: Fort Baker near Bridgeville (Cooper, 1960); Angelo Preserve, UC NCCRP (Kotanen, 1996, 1997, 2004); UC Hopland field station (Heady, 1956); Bodega Bay (Alpert & Maron, 2000; Maron & Jefferies, 2001; Kolb *et al.*, 2002); Tomales Bay (Reynolds *et al.*, 2001; Corbin & D'Antonio, 2004b, a; DiVittorio *et al.*, 2007); Marin county (Huntsinger *et al.*, 1996); Contra Costa county and East Bay (Bartolome & Gemmill, 1981; Huntsinger *et al.*, 1996; Bartolome *et al.*, 2004); Jasper Ridge and Stanford (McNaughton, 1968; Dukes, 2002; Buisson *et al.*, 2008); Santa Clara (Huenneke *et al.*, 1990); Pomponio State Beach Park (Hatch *et al.*, 1999; Fehmi & Bartolome, 2003); Santa Cruz (Hayes & Holl, 2003; Buisson *et al.*, 2006); Monterey county (Robinson, 1971; Knops *et al.*, 1995, 2002; Stromberg & Griffin, 1996; Stromberg & Kephart, 1996; Hamilton *et al.*, 1999; Stromberg *et al.*, 2001). A good number of reviews or large scale studies have also been

written on the subject: (Heady *et al.*, 1988; D'Antonio *et al.*, 2002; Hayes & Holl, 2004). These studies show that disturbances in coastal prairies include changes in fire and grazing regimes, intensive cultivation and the introduction of competitive exotic plant species (Comer *et al.*, 2022). Disturbances may also include the combination of heavy grazing with recurrent years of drought around 1862-64.

While coastal prairies seem to have a better resilience than inland grasslands (e.g. Heady *et al.*, 1988) and while some northern California prairies, where disturbance was moderate, show relatively high resilience (e.g. Kotanen, 2004), most Californian coastal prairies have been sufficiently impacted that their recovery is extremely slow (Hamilton *et al.*, 1999) or even unlikely (Stromberg & Griffin, 1996). Since coastal prairies have changed as a result of several disturbances, their recovery cannot be triggered by re-introducing grazing alone (Bartolome & Gemmill, 1981; Stromberg & Kephart, 1996), by just sowing native plant seeds (Hamilton *et al.*, 1999), or by simply reducing soil nitrogen (Alpert & Maron, 2000; Corbin & D'Antonio, 2004a). Restoration thus needs to include various combinations of treatments (Stromberg *et al.*, 2007). Exotic species seem to be the biggest issue in prairie restoration as they out-compete native species at all stages: they germinate earlier (Chiariello, 1989), and this in spite of the germination cues to reduce time of emergence provided by some annuals to *S. pulchra* (Dyer *et al.*, 2000). Also, exotic annual grasses grow faster in the spring, reach maturity first (Bartolome & Gemmill, 1981) and can set more seeds (Nelson & Allen, 1993).

The Stanford site

The Stanford site is located in the Stanford foothills, south of Junipero Sierra at the junction of Stanford Avenue (Figure 2). Before European settlement, Ohlone people lived in the area of the San Francisquito Creek, fishing and gathering acorns (Gullard & Lund, 1989; Stanford Historical Society, n.d.). On the plain lying between the coastal mountain range and the South Bay, grasslands are believed to have been dominated by *Leymus triticoides*, while on the hills east and west of the Bay, *Stipa pulchra* must have dominated grasslands (Holstein, 2001). Relicts of both types of grasslands can still be found in these



Figure 2 – Location of the Stanford site on the Stanford campus foothills (©Google2022).

places. Our study site being in the hills we suppose that *Stipa pulchra* was the dominant bunchgrass in the area, especially since it can still be found on and around the site.

In 1769, Portola's expedition reached Palo Alto (Spector, 1994). Mission Santa Clara was established ~20 km away in 1777. The area around Stanford was divided in three large ranches: Rancho San Francisquito, Rancho Rincon de San Francisquito and Rancho Rinconada del Arroyo de San Francisquito (Spector, 1994).

Rancho de San Francisquito was located mainly on the west bank of Arroyo San Francisquito where is now western Menlo Park and on the northwest end of Stanford University campus. This ~600 ha ranch belonged to Antonio Buelna from 1839 to 1863. It was then purchased by George Gordon and sold to Leland and Jane Stanford around 1885 (Buisson, 2005; Anonymous, n.d.). Rancho Rincon de San Francisquito, laying from southern Palo Alto to the hills and including most of Stanford campus first belonged to Jose Pena. In 1841, Segundino Robles purchased part of the land, Pena seems to have kept the land towards the hills as an 1862 map shows Pena's house near Lake Lagunitas. Whether this is right or not, both men had cattle. Rancho Rinconada del Arroyo de San Francisquito was located northeast of Rancho Rincon de San Francisquito, where is now Menlo Park and downtown Palo Alto. This ranch covered between 900ha and

5,000ha depending on authors and belonged to Rafael Soto and his family (from before 1839 to 1872) (Donnelly, 1994; Buisson, 2005; Anonymous, n.d.). In 1850, John Greer married M. L. Soto (Spector, 1994) and made business from lumber and tallow and thus bred cattle or sheep (Donnelly, 1994). These three ranches bred numerous cattle and during the dry years, there was rarely a sufficient amount of pastures for all the horses and cattle (Ballard, 1894). A description of the Stanford area given by Antonio Buelna in 1837 said that the land was covered with white oak (*Quercus lobata*), coast live oak (*Quercus agrifolia*) and an underbrush called chamisal (some type of chaparral) and that the hills were grazed by a few hundred cattle (Ballard, 1894). By the 1850's, more people settled and started ranching more intensively on the hills while cultivating wheat and barley on the flat land. About 10 years later land was cleared for timber (Ballard, 1894).

Leland and Jane Stanford purchased a total of 3300 ha of land that was given to the University in 1885. Some 1000 ha of hills located between Highway 280, Page Mill and Sand Hill Roads where our site is located were lightly used lands (Buisson, 2005). Disturbance history could not be described more precisely with aerial photographs from 1928, 1948 and 2002 because they are not sufficiently detailed.

The UCSC site

The study site is located at the junction of Coolidge and Hagar Drive, on UCSC campus, and is on a marine terrace, ancient ocean floor that was uplifted (Figure 3). The site has a ~70 cm deep A horizon of loamy soil (clay, silt and sand) and a ~100 cm B horizon of clay, overlaying landslide, stream and wind-blown deposits, overlaying marine terrace deposits (gravel and sand) (Stanley, 1982).

Before 1791, the Santa Cruz area was home to about 1,000 Ohlone people who lived from gathering, harvesting and hunting, for which they managed grasslands (Jarrell, 1982). Mission Santa Cruz was settled in 1791. Agriculture was its main economic activity (Kimbrow *et al.*, 1985): it produced wheat, corn, barley, beans, garbanzo beans and peas and bred numerous cows, sheep, goats, pigs, horses and mules (Table 1).

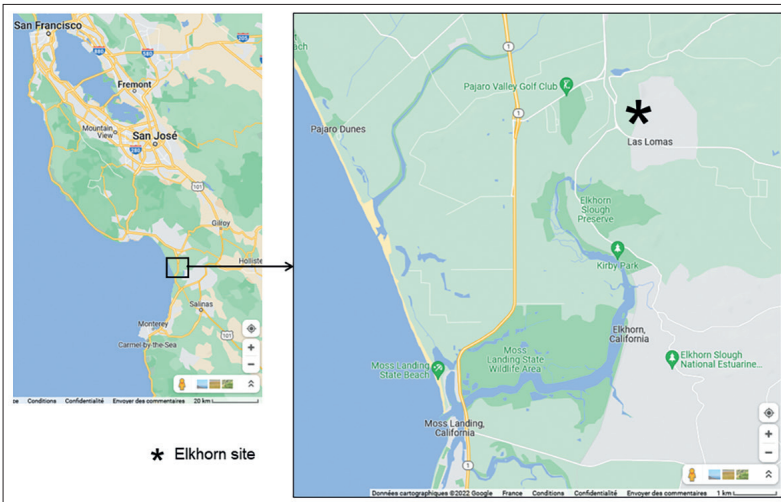


Figure 5 – Location of the Elkhorn site south of the city of Watsonville (©Google2022).

valley occurred around 1770. Like elsewhere during the Spanish-Mexican period, livestock (cattle, sheep and horses) supported most of the economy. Don Ignacio Vicente Ferrer Vallejo received the grant of Rancho Bolsa de San Cayetano in 1824. Its limit to the north

is the Pajaro River, to the south an estuary separating it from the Rancho Carneros, to the east Rancho Vega del Rio del Pajaro and to the west the Monterey Bay (Hoover *et al.*, 1937) (Figure 6). It included what is now part of the Porter estate and other important estate and it seems like Don Ignacio had cattle on the ranch for several years (Atkinson, 1934). Although only 40 people (count excluding native people, number unknown) lived in the Pajaro Valley the mid 19th century, cattle, sheep and horses were raised in very large numbers in the area (Gordon, 1974). José de Jesus Vallejo, Don Ignacio eldest son, may have lived on his father ranch until around 1870 (Hoover *et al.*, 1937), and bred cattle (Lydon, 1989) around which time the land was purchased by J.T. Porter.

Changes in the landscape of the area occurred between 1840 and 1880, while California became part of the United States (1848) (Figure 6). In 1840, the main land-use was cattle grazing on big ranches (average 7000 ha), where crops were limited to domestic consumption. While agriculture developed around the 1870's in California, it only really started around 1890 in the Monterey area and the Pajaro Valley. Land-use was diversified emphasizing beets on fertile soil and grains elsewhere (Gordon, 1977). Small farms of ~40 ha developed, on which various crops (grains, vegetables, fruits) were grown for domestic and commercial consumption (Hornbeck, 1969) (Figure 7).

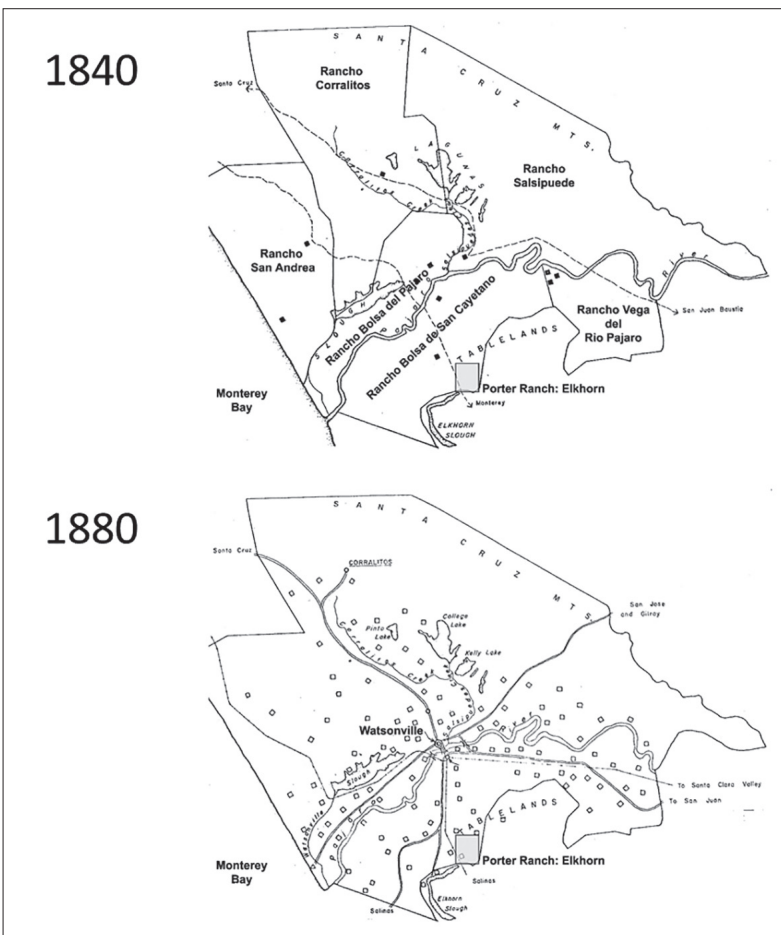


Figure 6 – 1840 cover map of the Pajaro Valley with Rancho boundaries, ranchsteads and trails. 1880 cover map of the Pajaro Valley with farmsteads and roads (Hornbeck 1969). The Elkhorn site is located on the map.

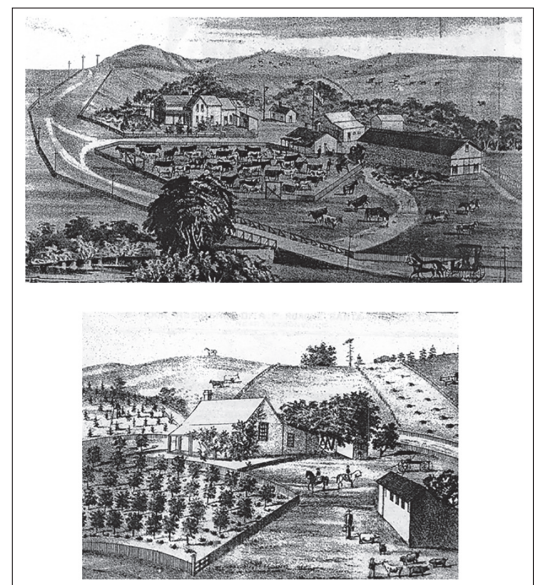


Figure 7 – Type of ranch in the vicinity of Santa Cruz at the end of the 19th century (Martin, 1879).

In 1879, the land of ranchos Rio Vega del Pajaro and Bolsa de San Cayetano was largely under cultivation either by the owners or by tenants (Martin, 1879). The Porter farm had two main activities: i) sugar beet and other commercial crops were grown in the valley (Pajaro Valley); and ii) the dairy was in Las Lomas, on the hills above the homestead, where the study site is located (Figure 7). Hay and grains were grown in Las Lomas as well as a bit of vegetable and fruits for domestic consumption (Zembsch, n.d.). T. Porter (J.T. Porter's grandson) sold 80ha of Las Lomas around 1930 to pay taxes, but the dairy remained. We can assume that the study site has been grazed since 1770, first moderately since cattle roamed freely and more intensively and continuously since 1820 by dairy cattle, beef cattle and horses (riding or work horses) (Zembsch, n.d.).

Recent cultivation history was compiled from aerial photographs (1931-2001) (Figure 8). Elkhorn was partly cultivated before 1931 when the first aerial photograph was taken. According to the owner, it was cultivated with artichokes around 1940, although from aerial photos, it seems more likely to have been hay. This site may not have been entirely cultivated, at least recently.

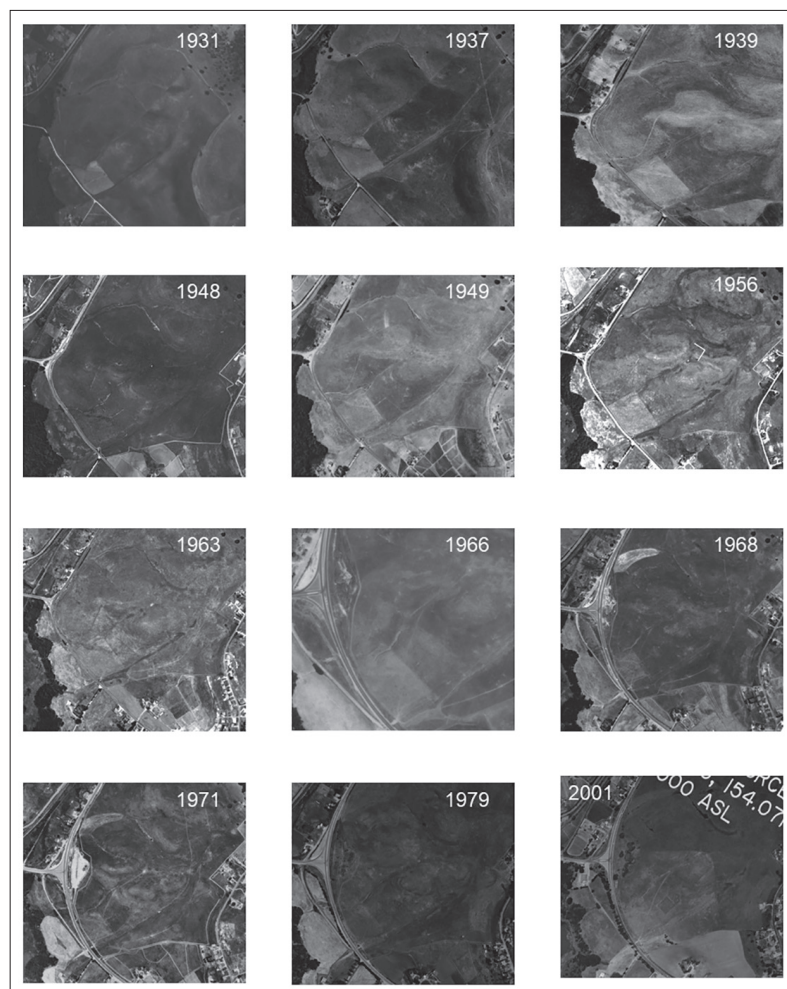


Figure 8 – Historical trajectory of the Elkhorn site from 1931 to 2001 from aerial photographs.

Conclusion

When restoring degraded grasslands, the reference ecosystem selected for restoration can aim for the potential natural vegetation, here coastal scrub or chaparral (e.g. Cione *et al.*, 2002), or for the semi-natural vegetation, as it was managed by native people, i.e. oak woodland or savannas (e.g. Montalvo & Ellstrand, 2000; Brooks & Merenlender, 2001) or coastal prairies (e.g. Hatch *et al.*, 1999; Corbin & D'Antonio, 2004a). The final decision must take into account today's needs and uses, future potential changes, and also historical records of what the site was like before degradation. This historical ecology study shows that these three sites most likely were grasslands or oak savannas before European settlement. All three sites were used for ranching and sometimes overgrazed. At least two of them were cultivated (the UCSC site and part of the Elkhorn site), probably leading to restoration being harder there (Robertson, 2004; Buisson *et al.*, 2006, 2008): plowing eliminates perennial species (Hamilton *et al.*,

2002; Stromberg *et al.*, 2007), destroys the native seedbank (Bekker *et al.*, 1997), drastically changes soil characteristics and soil microbial community composition on a long-term basis (Steenwerth *et al.*, 2003; Jaunatre *et al.*, 2016). As mentioned by Robertson (2004), concentrating restoration efforts on grasslands that have not been cultivated is probably more cost-efficient. Hamilton *et al.* (2002) also demonstrated that *Stipa pulchra* stands found in areas that have never been cultivated are healthier than those in areas that have been disturbed (shorter-lived, low basal cover, low seedling recruitment). This said, we managed to experimentally reintroduce native bunchgrasses at the three sites (*Stipa pulchra* at the Stanford site (Buisson *et al.*, 2008) and *Danthonia californica* at the UCSC and Elkhorn sites (Buisson *et al.*, 2006)) by considerably reducing the competition from invasive species *via* topsoil removal, a technique which should only be used in sites with no native seed bank.

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