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SPATIAL PATTERNS OF VEGETATION CHANGE IN A FIRE-SUPPRESSED COASTAL CALIFORNIA LANDSCAPE

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ABSTRACT

California's central coast contains high species richness and plant endemism that is threatened by ongoing land use and climate change. Better understanding of regional vegetation dynamics is needed, where its vegetation mosaic and stand succession interact with a strong Mediterranean climate, wildfire, and grazing. We examined what historical data could reveal about these interactions by using two lines of evidence—historical aerial photographs from 1938 and vegetation maps surveyed in the 1930s—and comparing them to other photographs and maps up to 2015. We used the recently established Jack and Laura Dangermond Preserve as the study area. The Preserve, stretching from the coast near Point Conception to the Santa Ynez Mountains, encompasses chaparral, grassland, oak woodlands, coastal scrub and closed-cone pine vegetation types. We asked what long-term vegetation change has occurred, and if we could detect the influences of wildfire frequency and grazing pressure. Across the 80-year time period, we found that grassland cover decreased by 26%, while shrubland and oak woodland cover increased by 31% and 16%, respectively. Our results were consistent across both historic datasets, lending confidence to the trends observed over time. These trends are consistent with other similar analyses along coastal California, supporting the long-held hypothesis that coastal grassland communities, and their unique biodiversity values, are lost as grazing and fire decrease. Our results motivate future work on the restoration of native grassland species and point to the possibility of using designed spatial patterns of coastal California vegetation mosaics to preserve long term habitat dynamics for the region's native plant communities in this biodiversity hotspot.

Key Words: Climate change, coastal California, historical ecology, land cover change, landscape ecology, shrubland encroachment, Wieslander VTM survey, wildfire.

California's central coast is characterized by a vegetation mosaic of oak woodlands, scrublands, chaparral, and grasslands (Keeley et al. 2011). These areas are of significant conservation importance due to their high levels of endemism (Thorne et al. 2009; Burge et al. 2016) and relative intactness. In some locations, vegetation is correlated with physical factors such as topography and geological substrate (Callaway and Davis 1993; Cole 1980), microclimates (Harrison et al. 1971), and fluctuations in annual climate, including climate change-intensified drought (Sousa et al. 2022).

Biotic interactions and disturbances such as wildfire and grazing also influence vegetation patterns in California's coastal chaparral (e.g., Van Dyke et al. 2001) and grasslands and prairies (Siegel et al. 2022; Hatch et al. 2002; Stromberg et al. 2001). In coastal California, observations about the effects of grazing and wildfire on grassland ecosystems suggest that in the absence of either or both factors, these systems can transition to chaparral and oak or other woodlands (McBride 1974; Callaway and Davis 1993, 1998). Grazing can be used in a sustainable fashion, although it is dependent on intensity and environmental conditions (Stahlheber and D'Antonio 2013). Fire was traditionally used for land management by Native Americans, but suppression of wildfire starting around 1910 (Cermak 2005) led to changes in fuel loads and fire frequencies (Steel et al. 2015), and potentially other types of vegetation change.

In terms of the spatial patterns of vegetation mosaics, grasslands in the Los Angeles Basin, for example, were found to increase with increased fire and grazing, but these grasslands were invadable by coastal sage scrub when fire and grazing were infrequent (Freudenberger et al. 1987), potentially driven by the grassland and coastal sage scrub's varying tolerances to and the frequency of disturbance. The advent of invasive grass species, in contrast, has led to higher fire frequencies, which has led to dieback of shrub, scrub, chaparral and other vegetation types in California (Keeley et al. 2011; Fusco et al. 2019). Climate change and associated intensified drought are also having large impacts on vegetation communities. For example, at our study site, the Jack and Laura Dangermond Preserve, Sousa et al. (2022) used remote sensing and modeling to quantify oak woodland cover changes from 1982–2000, identifying that as droughts occurred, the extent of dieback in different parts of the oak woodlands changed differentially in response to underlying land conditions, including geology, soils, and topography. An understanding of the stability of the spatial patterns of vegetation in Central Coastal California could help disentangle the relative influences of wildfire, grazing, and climate change (e.g., drought), which in turn could provide context for resource managers focused on the preservation or enhancement of selected habitats.

The objective of this study was to identify historical trends in the extent and structure of terrestrial habitat types at the Jack and Laura Dangermond Preserve. We analyzed historic aerial photographs from 1938, 1978, and 2012 and vegetation maps from 1931 and 2015 to determine the change in cover of three broad habitat types: grassland, shrubland, and woodland. The Preserve, like most of California, experienced a severe drought from 2012–2020 (Sousa et al. 2022); however, it is unlikely that land cover, especially that of trees and shrubs, changed significantly enough to impact to impact the 2012 aerial photography map or the 2015 vegetation map we used, and subsequently the results of this study. By using two separate but parallel data sources, we are able to have increased confidence in any habitat trends we observe at the Preserve over time. We also compared habitat type transition rates between areas of the Preserve that have and have not been exposed to fire. We discuss how understanding long-term dynamics in these habitat types can inform vegetation management strategies and conservation priorities in protected areas like the Dangermond Preserve.

Study Area

The study area occupies the approximately 9,860 ha (24,364 acres) Jack and Laura Dangermond Preserve (hereafter, the Preserve) in Santa Barbara County, which is owned by The Nature Conservancy (TNC). Protected in 2017, the Preserve represents a relatively intact piece of coastal California habitat, located at Point Conception, as the boundary between the Central and South Coast Ecoregions (Fig. 1). The property is bordered by Vandenberg Space Force Base and Jalama Beach County Park to the north and west, and Hollister Ranch to the east. Elevation ranges from sea level to approximately 515 meters at the crest of the Santa Ynez Mountains. The climate is Mediterranean, with mean annual precipitation, nighttime low, and daytime high temperatures over time as follows: 1930–1939, 46.0 cm precipitation, 8.3° C nighttime low, 20.3° C daytime high; 1970–1979, 48.7 cm precipitation, 8.5° C nighttime low, 20.1° C daytime high; and for 2010-2019, 42.8 cm precipitation, 10.1° C nighttime low, 20.0° C daytime high, a period that includes the first seven years of California's intensive 2012–2020 drought (Griffin & Anchukaitis 2014) (data from PRISM [Daly et al. 2001], downscaled using the Basin Characterization Model [Flint et al. 2013; Thorne et al. 2015]).

Over 600 plant and animal species occur on the property, of which 58 have a conservation status, including 13 that are threatened or endangered (Butterfield et al. 2019; Appendix S1). Vegetation communities at the Preserve are representative of those found more broadly along coastal California. Coast Live Oak (*Quercus agrifolia* Née) woodland is the dominant oak vegetation type (Butterfield et al. 2019), covering approximately 2,440 hectares (6,029 acres) (WRA Inc., 2017). For the purposes of this study, vegetation classified as Coast Live Oak forest and woodlands is characterized by greater than 20% tree cover and greater than 50% relative tree cover (Sawyer et al., 2009). It is common in both upland and bottomland areas of the Preserve, where it forms a mosaic with other vegetation alliances. The shrublands include scrub communities, with medium height, soft-woody shrubs, and chaparral communities, with medium to tall, hard-leaved, woody shrubs. The most common scrub species are California Sagebrush scrub and Coyote Brush scrub. The most common chaparral species are Toyon (*Heteromeles arbutifolia* (Lindl.) M.Roem) and La Purisima Manzanita (*Arctostaphylos purissima* P.V.Wells). The Preserve's grassland extent consists of approximately 95% non-native annual grasslands, 4% purple needlegrass grassland, and less than 1% giant wild rye grassland (Butterfield et al. 2019).

The Preserve has been grazed for more than 200 years dating back to the Rancho era. The Preserve has more detailed records from the contemporary era, 1913 to present. During this time period, stocking rates and grazing approaches have varied significantly, driven by climate, vegetation productivity, cattle industry forces, and adopting approaches to grazing for conservation goals and objectives. As an example, in 1913, the Preserve was stocked with 565 cattle, 143 horses, 9 bulls, and 2 stallions (PHR Associates 1990). Cattle numbers climbed as high as 1,630 cattle in the 1940s, and stabilized between 900 and 1,200 through the 1970s and 1980s. Historically, the carrying capacity for the Preserve was approximately 1,680 animal units in an average rainfall year (PHR Associates 1990, Butterfield et al. 2019). Stocking rates since 2017 have been lower, between 500 and 1,000 animal units, driven primarily by prolonged drought and lack of water and forage (Butterfield et al. 2020).

Methods

Data Preparation

Aerial photographs. The aerial photograph analysis used images from January 1938, January 1978,

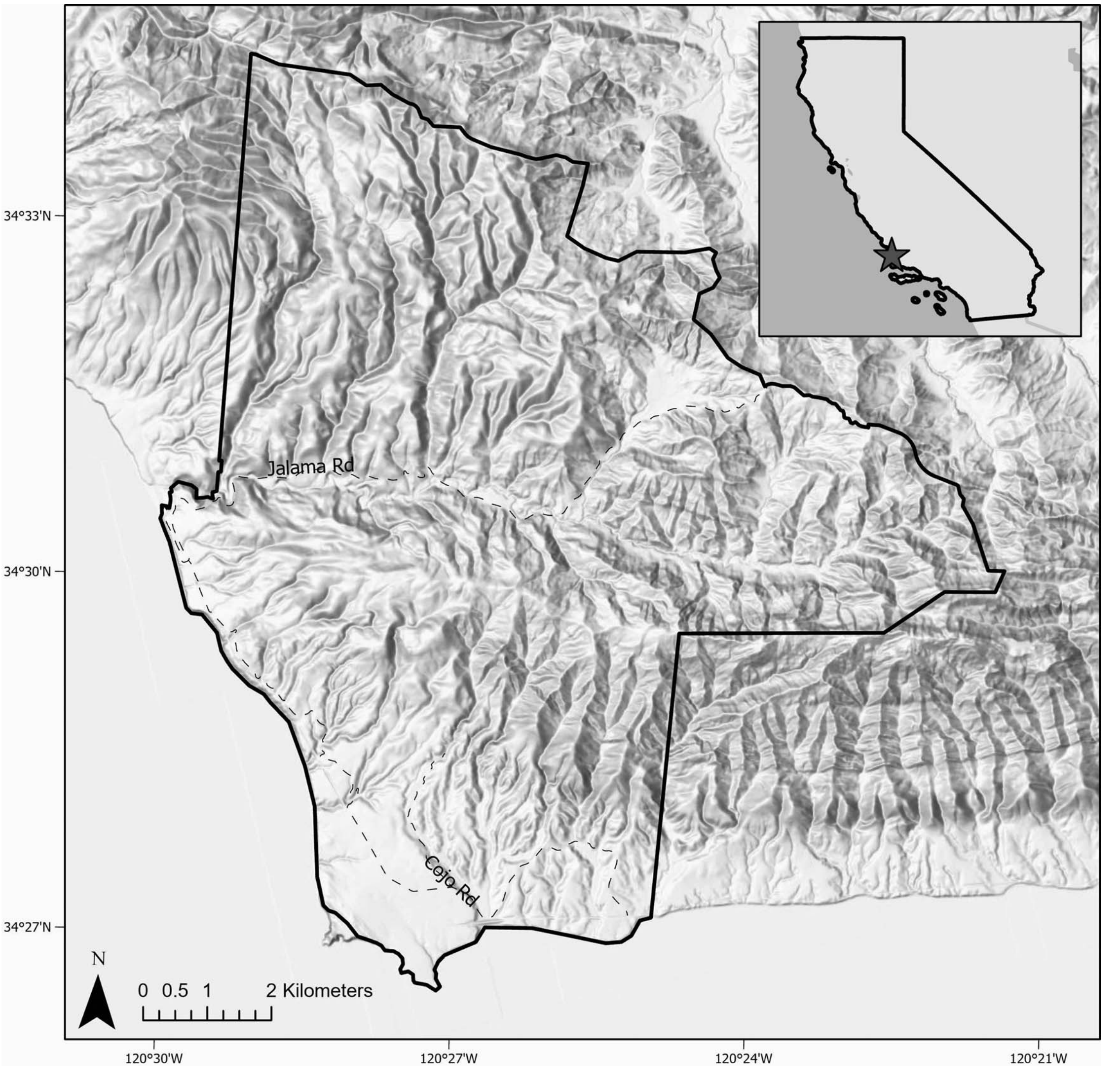

FIG. 1. Overview map of the Jack and Laura Dangermond Preserve. The approximately 9,860 ha (24,364 acre) Preserve, outlined in black, is located at Point Conception in western Santa Barbara County.

and May 2012 (Fig. 2; Appendix S2) to track changes in habitats over time. These years were selected for their complete coverage of the study area.

The 2012 photographs were available as georeferenced and orthorectified images. The 1938 and 1978 photographs were not georeferenced and required georeferencing to properly align them with the 2012 images. The images were georeferenced in ArcGIS version 10.6.1 using stable and identifiable features such as buildings, intersections between roads and/or creeks, and ridgelines as ground control points (GCPs). A total of 10 to 69 GCPs were chosen for each image; a higher number of GCPs were selected for the 1938 images that lacked human-built features. Georeferencing was completed with a second-order transformation to minimize root mean square error (RMSE) of actual GCP location. The second-order transformation shifts, bends, and/or curves the raster data (Esri 2018), and it can compensate for original image capture issues, such as camera tilt. After second-order transformation, the average RMSE across the 11 images from 1938 was 59 meters, and the average RMSE across the five images from 1978 was 48 meters (Appendix S3). The highest RMSE across all photos was 78 meters.

We identified the habitat type at 340 sample points within the study area (Fig. 3). We used the same sample points in all three sets of photos to assess if the habitat type changed over time at each location. Sample points were generated using the Create Random Points tool in ArcGIS version 10.6.1. Due to likely spatial errors resulting from georeferencing, images

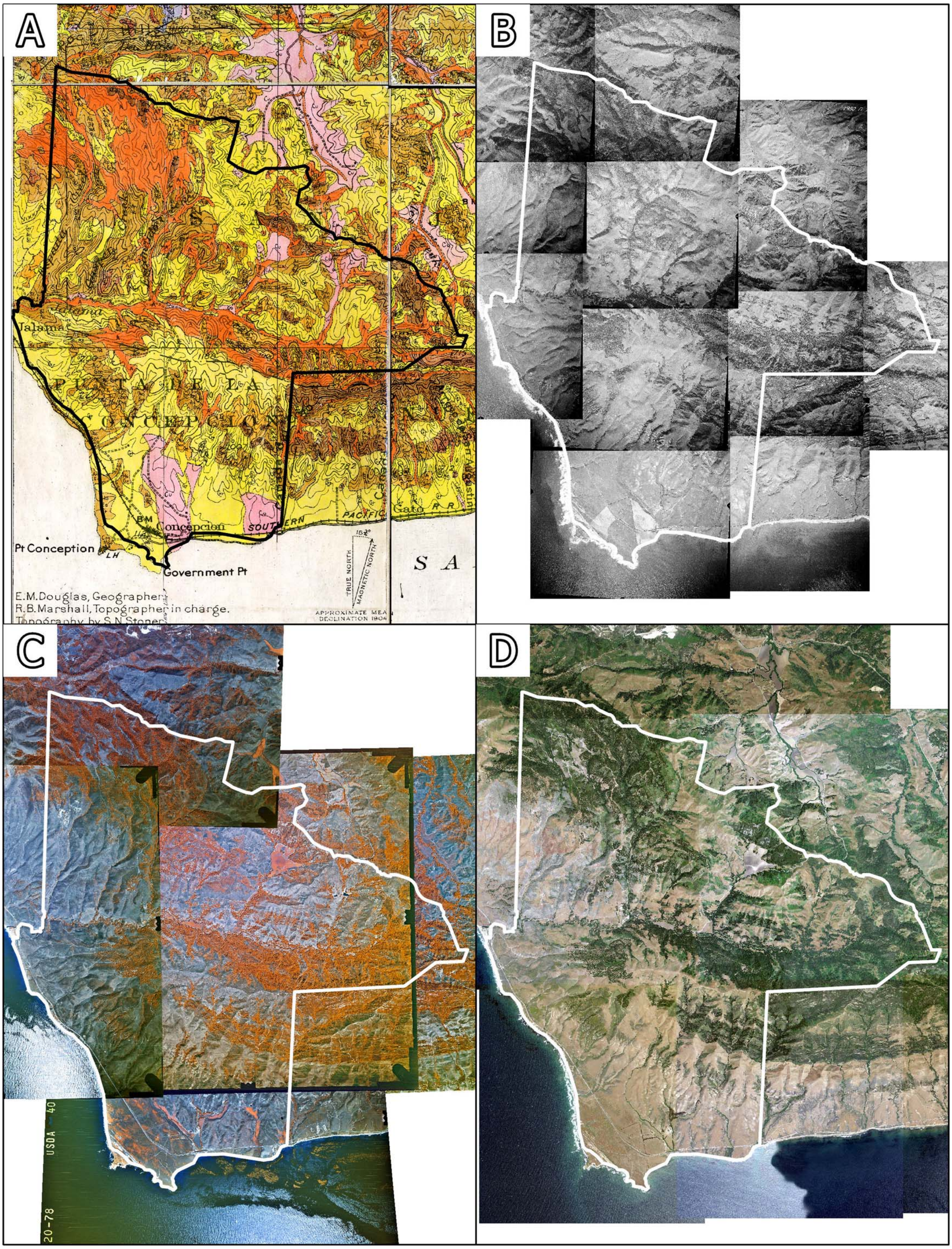

FIG. 2. Historical imagery used to identify habitat types at the Dangermond Preserve. A: 1931 topographic map with hand-drawn species composition and habitats from the Wieslander Vegetation Type Maps (VTM); colors represent different vegetation communities, with dominant species identified by 1-2 letter codes (Kelly et al. 2005; Thorne and Le 2016). B: 1938 black and white aerial photographs (Fairchild Aerial Surveys 1938). C: 1978 false color aerial photographs (Pacific Aerial Surveys 1978). D: 2012 color aerial photographs (USDA-FSA Aerial Photography Field Office 2012). Additional information regarding visual interpretation of habitats in Panels B–D is provided in supplemental materials (Appendix S4).

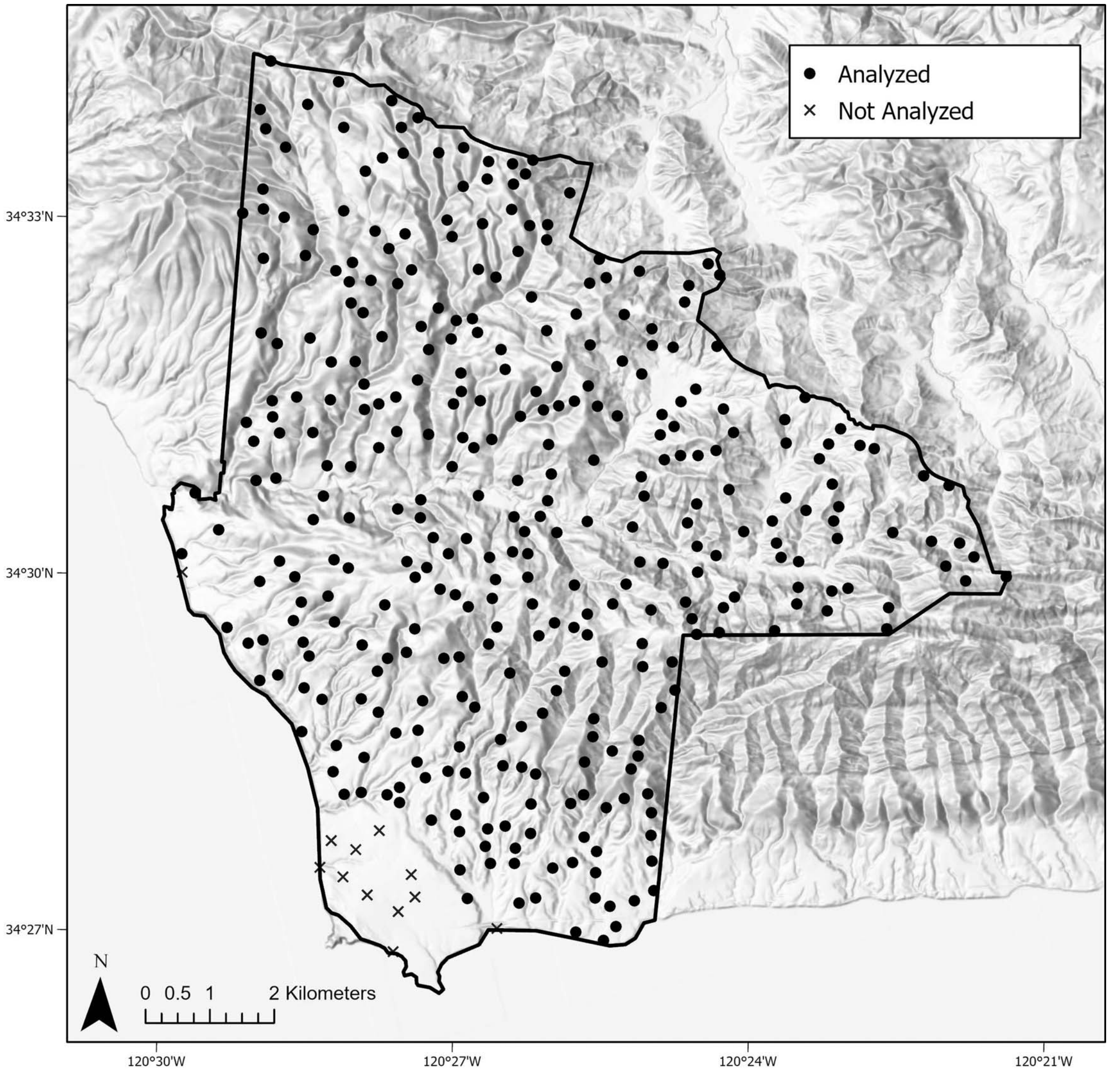

FIG. 3. Distribution of random sample points at the Dangermond Preserve for aerial photograph analysis. Black points (n = 340) were retained for the analysis. Black X's were excluded because they were on a beach (n = 3) or appeared to be dominated by *Carpobrotus edulis* (ice plant) (n = 9), a widespread invasive species in this area of the Preserve.

from different years may not always align perfectly, meaning that differences in habitat type identified at a sample point between two years could simply be due to the RMSE. To account for this, we created a grid around each sample point, using an ArcGIS toolbox created by Dilts and Hornsby (2016). The distance from a sample point, centered in the grid, to the side of its grid is 80 meters. This size was chosen based on the largest RMSE of 78 meters. Therefore, the grids are 160 by 160 meters, and each cell within a grid is 32 by 32 meters (Fig. 4). In order to have independent random samples, we did not allow grids to overlap. Given that the distance from the sample point to a vertex of its grid is 113.14 meters (Fig. 4), we set the minimum allowed distance between sample points to 226.3 meters. In restricting overlap, 352 points were generated. Later, 12 points were excluded—including three that fell on the beach and nine that were dominated by Freeway Ice Plant (*Carpobrotus edulis* (L.) N.E. Br.), a widespread invasive species in this area of the Preserve—leaving 340 total sample points (Fig. 3). Ice Plant areas were left out of this analysis because 1) if present, it was difficult to distinguish Ice Plant in the black and white images from 1938, which could introduce bias, and 2) as a succulent, Ice Plant does not fall into our three broad habitat types.

We visually classified habitat in the sample point-associated grids to four broad habitat types: woodland, shrubland, grassland, and other, where the image showed bare ground, rocky cliffs, roads, or train tracks

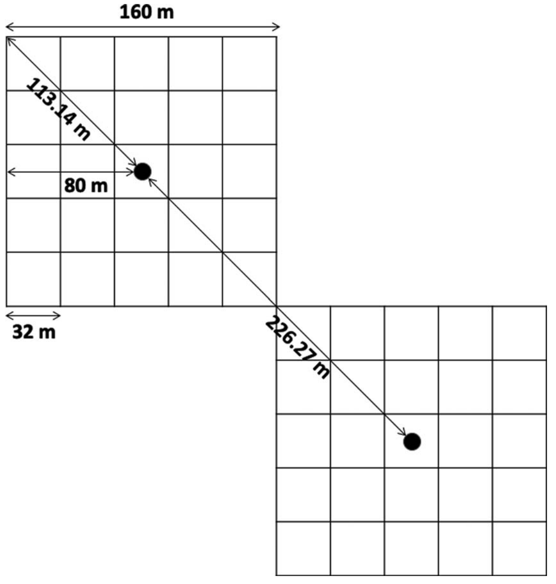

FIG. 4. Diagram of sample grids centered on randomly generated sample points. The operational grid scale for the photographic analysis is 160 square meters. The distance from a sample point to a vertex of its grid is 113.14 meters, so the minimum allowable distance between sample points was set to 226.27 meters to avoid grid overlap.

(Appendix S4). Shrubland conservatively included both coastal scrub and chaparral vegetation types because we could not reliably distinguish the two in our visual interpretation of the photographs. Within each 160 by 160m grid we identified the habitat type that occupied the greatest proportion of the 25 smaller 32 by 32m cells that made up each grid. For example, if nine cells are woodland, four cells are shrubland, and 12 cells are grassland, the dominant type at that point was labeled grassland. Where multiple habitat types were equally dominant, such as 12 woodland, 12 shrubland, and one "other", we recorded the dominant type as "tie." There were six ties in 1938, 11 in 1978, and two in 2012.

Vegetation maps. Changes in habitat extent tracked on vegetation maps used two time periods: the historic Wieslander Vegetation Type Map (VTM) from 1931 (Kelly et al. 2016; Thorne and Le 2016) and a map from 2015 (California Department of Forestry and Fire Protection [FRAP] 2015).

The VTM survey recorded vegetation across about half of California with maps, vegetation plots, and photographs (Wieslander 1935). The plot data have been used to document change in chaparral density (Franklin et al. 2004), changes in Southern California conifer forest stand structure (Minnich et al. 1995), increases in oaks and declines in pines regionally (Goforth and Minnich 2008) and statewide (McIntyre et al. 2015), change in forest carbon (Fellows and Goulden 2008), and to identify a zone of climatically no-longer suitable establishment conditions for low-elevation conifers (Hill et al. 2023), among many others. The VTM's maps have also been used extensively, including to develop range maps of California tree (Griffin and Critchfield 1972) and shrub species (Sampson and Jespersen 1963) and to inform the species composition and polygon boundaries for parts of California's first digital map of existing vegetation (Davis et al. 1998). The maps have also been used as a baseline to examine change in vegetation extents on conservation lands of different decades in the San Francisco Bay area (Santos et al. 2014) and to document the upslope retraction of ponderosa pine-dominated forests in foothills of the Sierra Nevada Mountains (Thorne et al. 2008). Freudenberger (1987) used the VTMs in parallel with aerial photos in the Los Angeles basin and found expansion of grasslands at the expense of shrublands.

Before comparing the VTM and FRAP vegetation maps, we took steps to improve the alignment of the digitized VTM maps (base map and vegetation polygon map). When recording the locations of vegetation types, the VTM surveyors used a different topographic base map (NAD 27, Clarke's spheroid of 1866) than the FRAP map. To account for this, we re-projected the topographic map in NAD 83 Teale Albers and shifted the VTM base map 45 meters east and 150 meters north to improve its alignment with the coastline and roads, using the locations of road intersections on the VTM base map and a modern road map as a guide. Based on 31 ground control points at road intersections, the root mean square error (RMSE) prior to shifting was 172 meters, and the RMSE after shifting was 57 meters, indicating a better fit. Then, the VTM vegetation polygon map was shifted visually in the same way to improve alignment with the coastline (Appendix S5 and S6). ArcGIS Pro version 2.2 was used for map alignment and to convert the maps from polygon to raster format.

In our study area, the VTM survey identifies eight Wildlife Habitat Relationship (WHR) types (Mayer and Laudenslayer 1988), while the FRAP map has 13. To facilitate comparison with the results of our aerial photograph analysis, we aggregated these mapped vegetation types to three more general habitat types: woodland, shrubland, and grassland (Table 1). Four WHR types (barren, urban, lacustrine, and deciduous orchard) were omitted from our analysis as they did not correspond to any of these habitat types.

Frequency of Habitat Types

For the aerial photograph analysis, we tallied the number of grassland-, shrubland-, and woodland-dominated sample points in each year. We used McNemar-Bowker tests to determine if proportions of these habitat types changed significantly between 1938 and 1978, 1978 and 2012, and 1938 and 2012 (R version 4.1.2). The "other" and "tie" categories were left out of these tests. Results were evaluated at significance level $\alpha = 0.05$. Post-hoc McNemar tests were used for pairwise comparisons

TABLE 1. COMPARISON OF VEGETATION TYPES OCCURRING IN THE STUDY AREA IN 1931 (WIESLANDER 1935; KELLY ET A. 2016) AND 2015 (CALIFORNIA DEPARTMENT OF FORESTRY AND FIRE PROTECTION 2015). California Wildlife Habitat Relationship (Mayer and Laudenslayer 1988) vegetation types were aggregated to three main habitat types of interest: Grassland, Shrubland, and Woodland.

Habitat type	Vegetation type 1931	Vegetation type 2015
Grassland	Annual grassland	Annual grassland
	Cropland	Pasture
Shrubland	Coastal scrub	Coastal scrub
	Mixed chaparral	Mixed chaparral
	Chamise-redshank chaparral	–
Woodland	Coast oak woodland	Coast oak woodland
	Montane hardwood	Montane hardwood
	Valley foothill riparian	Valley foothill riparian
	–	Closed-cone pine cypress
	–	Montane hardwood conifer

of habitat types, using the Holm correction for multiple comparisons (R version 4.1.2).

We resampled both vegetation maps to 60 m resolution, which addresses two scale issues: the spatial accuracy of the VTM maps listed above and the finer-resolution of the 30 m FRAP map (Thorne et al. 2006). We then calculated the area of woodland, shrubland, and grassland habitat within the study area in 1931 and in 2015. For each habitat type, we also calculated the percent change in area from 1931 to 2015.

Transition Rates Between Habitat Types

For the aerial photograph analysis, we calculated transition rates between habitat types using paired data of a sample point's dominant habitat in an earlier year and its dominant habitat in a later year. For example, if 27 of 174 grassland points in 1938 transitioned to shrubland by 1978, the grassland-to-shrubland transition rate over this period was 16%. For the vegetation maps, we calculated transition rates between habitat types by stacking the 1931 VTM map and the 2015 FRAP map to see where habitat types changed or stayed the same over time, using an analogous calculation to the one used for the aerial photograph analysis. For the map analysis, we converted the vegetation maps to raster format at 60-meter resolution to account for the 57-meter RMSE in VTM map alignment (Thorne et al. 2006). This method addresses two issues with map comparison. First, it permits better assurance that the habitat recorded in each 60-m cell is well-enough located to represent what was actually at that location in the 1930s. Second, the finer-scale vegetation patterns in the 2015 map were generalized, by assigning the most spatially extensive type within each cell as the vegetation type in that cell. This reduces the chance that the transition analysis is confounded by the higher resolution of vegetation patches in the newer data.

To compare transition rates between the photo and map analyses, which have time periods of different length, we also calculated annualized rates, following the annualized deforestation rate equation used by Flamenco-Sandoval et al. (2007). For example, the annualized transition rate (ATR) from grassland to shrubland, over the period 1938 to 1978 (40 years), is calculated as:

$$\text{ATR }(\%/\text{year}) = \left[1-\left(1-\frac{\text{Grassland points that converted to shrubland}}{\text{Total grassland points in 1938}}\right)^{\frac{1}{40}}\right] \times 100$$

Using wildfire and prescribed burn perimeter data from FRAP (California Department of Forestry and Fire Protection 2017), we classified areas of the Preserve as "burned" if they have burned at least once since 1981 and "unburned" if they have not burned since then. Though the FRAP dataset may be an incomplete record of fires at the Preserve, it was the best available fire data at the time of this analysis (Fig. 5). Of the aerial photograph sample points, 114 had burned and 226 had not burned. Of the Preserve map raster cells (60-meter resolution), 9,358 are burned and 18,272 are unburned, meaning that 33.8% of the Preserve burned since 1981. We compared habitat type transition rates between burned and unburned areas.

RESULTS

Frequency of Habitat Types

Based on our analysis, since the 1930s the aerial extent of grassland has decreased, while shrubland and woodland have increased. In the 1930s grassland was the most common vegetation type across the Preserve, whereas in 2012 (aerial photographs) and 2015 (vegetation maps), the three habitat types (grassland, shrubland, and woodland) were more evenly represented (Fig. 6).

According to the vegetation map analysis, there has been a 26% net loss in grassland area from 1931

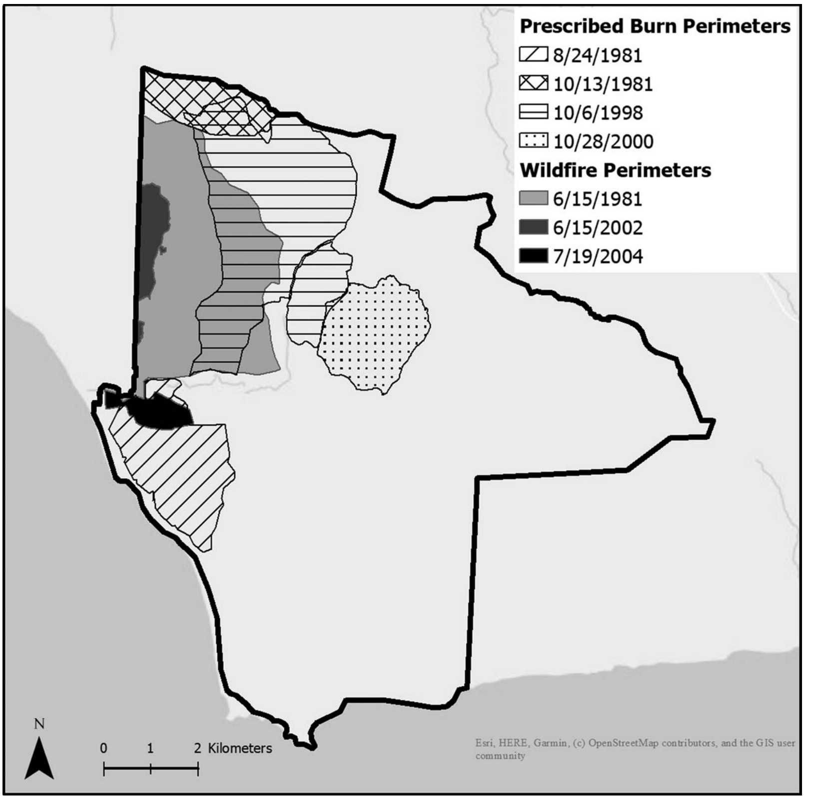

FIG. 5. Historical prescribed burns and wildfires at the Dangermond Preserve. Fire perimeters, clipped to the Preserve boundary, are from the Fire and Resource Assessment Program (FRAP) (California Department of Forestry and Fire Protection 2017).

to 2015, while shrubland area increased by 31%, and woodland area increased by 16% (Fig. 7). The aerial photograph analysis shows consistent results when looking at the proportion of sample points classified as woodland, shrubland, and grassland over the years. The proportion of woodland-, shrubland-, and grassland-dominated sample points changed significantly between 1938 and 1978 ($\chi^2(3) = 8.7886$ $P = 0.03$), 1978 and 2012 ($\chi^2(3) = 23.036$, $P < 0.001$), and 1938 and 2012 ($\chi^2(3) = 46.161$, df = 3, $P < 0.001$). This result is driven largely by a decrease in grassland and an increase in shrubland (Fig. 6). Post-hoc McNemar-Bowker pairwise tests of the grassland and shrubland points confirmed that shrubland increased at the expense of grassland over the whole period from 1938 to 2012 (Holm-adjusted $P < 0.001$) and specifically from 1978 to 2012 (Holm-adjusted $P < 0.001$), but not in the period from 1938 to 1978 (Holm-adjusted $P = 0.18$) (Table 2). All other pairwise tests were not significant.

Transition Rates Between Habitat Types

Over the entire study area, grassland-to-shrubland and shrubland-to-woodland transitions were the most common since the 1930s (Fig. 8 A–D). Similar grassland-to-shrubland transition rates are found in the photo analysis (0.51% per year) and the map-based analysis (0.40% per year) from the 1930s to the 2010s (Fig. 8A, B). However, the intermediary year (1978) provided by the photo analysis suggests that the prevalence of grassland-to-shrubland transitions was not consistent over this period. According to the photo analysis, shrubland-to-grassland transitions were more common from 1938 to 1978, with 0.56% per year of shrubland sample points that transitioned to grassland and 0.42% per year of grassland sample points that transitioned to shrubland (Fig. 8C). The signal reversed in the second time period (1978–2012), with 1.15% per year of grassland points that transitioned to shrubland and 0.45% per year of shrubland points that transitioned to grassland (Fig. 8D). (Detailed transition rates can be found in Appendices S7 through S9.)

Grassland-to-shrubland transitions were more common in burned areas than unburned areas of the Preserve (Fig. 8 E–H). The grassland-to-shrubland transition rate (1.93% per year) was about six times higher than the reverse transition rate (0.29% per year) in burned areas of the Preserve, whereas in unburned areas the forward (0.95% per year) and reverse (0.63% per year) rates were more similar,

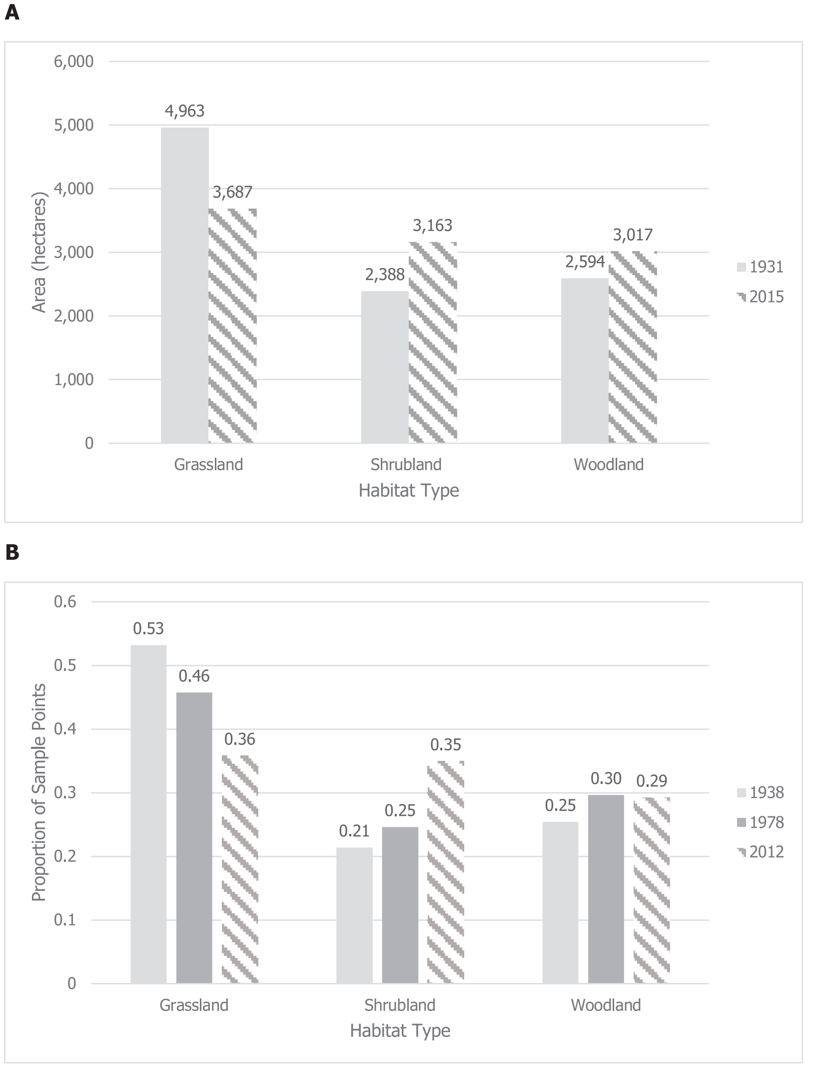

FIG. 6. Temporal change in proportion of habitat types in vegetation maps and aerial photograph sample points, showing parallel trends of increasing shrubland/woodland and decreasing grassland over time. Panel A: Area (hectares) of grassland, shrubland, and woodland in the study area in 1931 and 2015. Area was calculated using the 1931 VTM vegetation map and the 2015 FRAP vegetation map at 30-meter resolution. Panel B: Proportion of aerial photograph sample points dominated by grassland, shrubland, and woodland in 1938, 1978, and 2012. Sample points dominated by "other" or "tie" were excluded, leaving 327 points in 1938, 317 points in 1978, and 335 points in 2012.

according to the photo analysis (1978–2012) (Fig. 8E vs. F). The map analysis is directionally consistent with the photo analysis, with the grassland-to-shrubland transition rate about two times higher than the reverse in burned areas, whereas in unburned areas the forward and reverse rates were about equal (Fig. 8 G vs. H).

Shrubland-to-woodland transitions were more common in unburned areas than burned areas (Fig. 8 E–H). The shrubland-to-woodland transition rate was 0.53% per year in unburned areas compared to 0.22% per year in burned areas, according to the photo analysis (1978–2012). In the map analysis, 0.49% per year of shrubland transitioned to woodland in unburned areas compared to 0.23% per year in burned areas (1931–2015).

DISCUSSION

Over an 80-year period, the relative frequencies of different habitat types in this coastal vegetation complex have changed substantially. Since the 1930s, the overall area occupied by grassland has decreased, while shrubland and woodland area have increased.

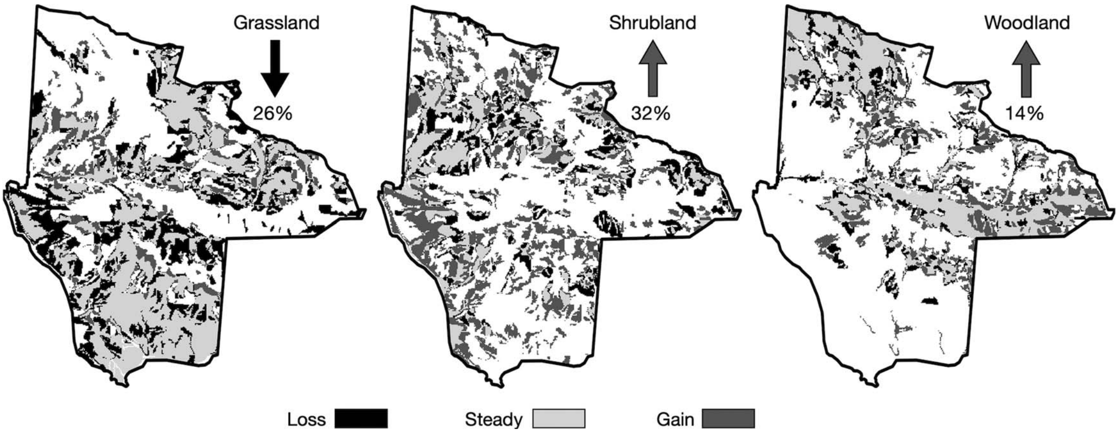

FIG. 7. Locations where grassland, shrubland, and woodland habitat have been lost (black), gained (light gray), or remained steady (gray) from 1931 to 2015. We stacked the 1931 VTM vegetation map and the 2015 FRAP vegetation map to generate this output. Percent change was calculated as the net gain or loss of habitat.

This conclusion is supported by both data sources, the vegetation maps, and aerial photographs.

The transition rate analyses suggest that these changes are in line with seral succession theory, with transition in environments with no disturbance of grassland to shrubland and shrubland to woodland (Wells 1962; Davis et al. 1988), in this case with climax seral vegetation consisting of Coast Live Oak woodlands, which comprise the majority of the trees on the Preserve (Sousa et al. 2022), and which can establish under shrubs (Callaway and Davis 1998; Zavaleta and Kettley 2006). These trends are consistent with other studies along the central and north coast of California (McBride and Heady 1968; Callaway and Davis 1993; Russell and McBride 2003; Keeley 2005; Hsu et al. 2012) and here are likely influenced by declines in grazing intensity (i.e., reduced stocking rates) (Butterfield et al. 2020), wildfire suppression, and fewer prescribed fire and shrub removal events by ranchers maintaining and opening land for grazing (common practices throughout the history of the region) (Butterfield et al. 2020).

The number of cattle on the property has decreased over time, with some fluctuation during drought conditions (PHR Associates 1990; Butterfield et al. 2020). Coincident with this decrease in cattle, our aerial photograph results suggest that grassland-to-shrubland transition became more prevalent during the 1978–2012 time period than it was previously from 1938–1978. Reduction of livestock grazing intensity has also been associated with grassland-to-shrubland transition in the San Francisco East Bay open spaces in observational (Russell and McBride 2003; McBride 1974) and experimental studies (McBride and Heady 1968).

TABLE 2. MCNEMAR-BOWKER TRANSITION TABLES FOR AERIAL PHOTO SAMPLE POINTS FROM 1938 TO 1978, 1978 TO 2012, AND 1938 TO 2012. Bold values represent statistically significant transitions ($P < 0.001$). Underlined values representing the dominant direction of transition. Values that are not bold represent statistically insignificant transitions.

		Post-transition 1978		
		Grassland	Shrubland	Woodland
Pre-transition 1938	Grassland	126	27	9
	Shrubland	14	42	10
	Woodland	3	5	73
		Post-transition 2012		
		Grassland	Shrubland	Woodland
Pre-transition 1978	Grassland	92	**47**	5
	Shrubland	**11**	57	9
	Woodland	6	6	82
		Post-transition 2012		
		Grassland	Shrubland	Woodland
Pre-transition 1938	Grassland	109	**55**	9
	Shrubland	**5**	55	10
	Woodland	4	4	75

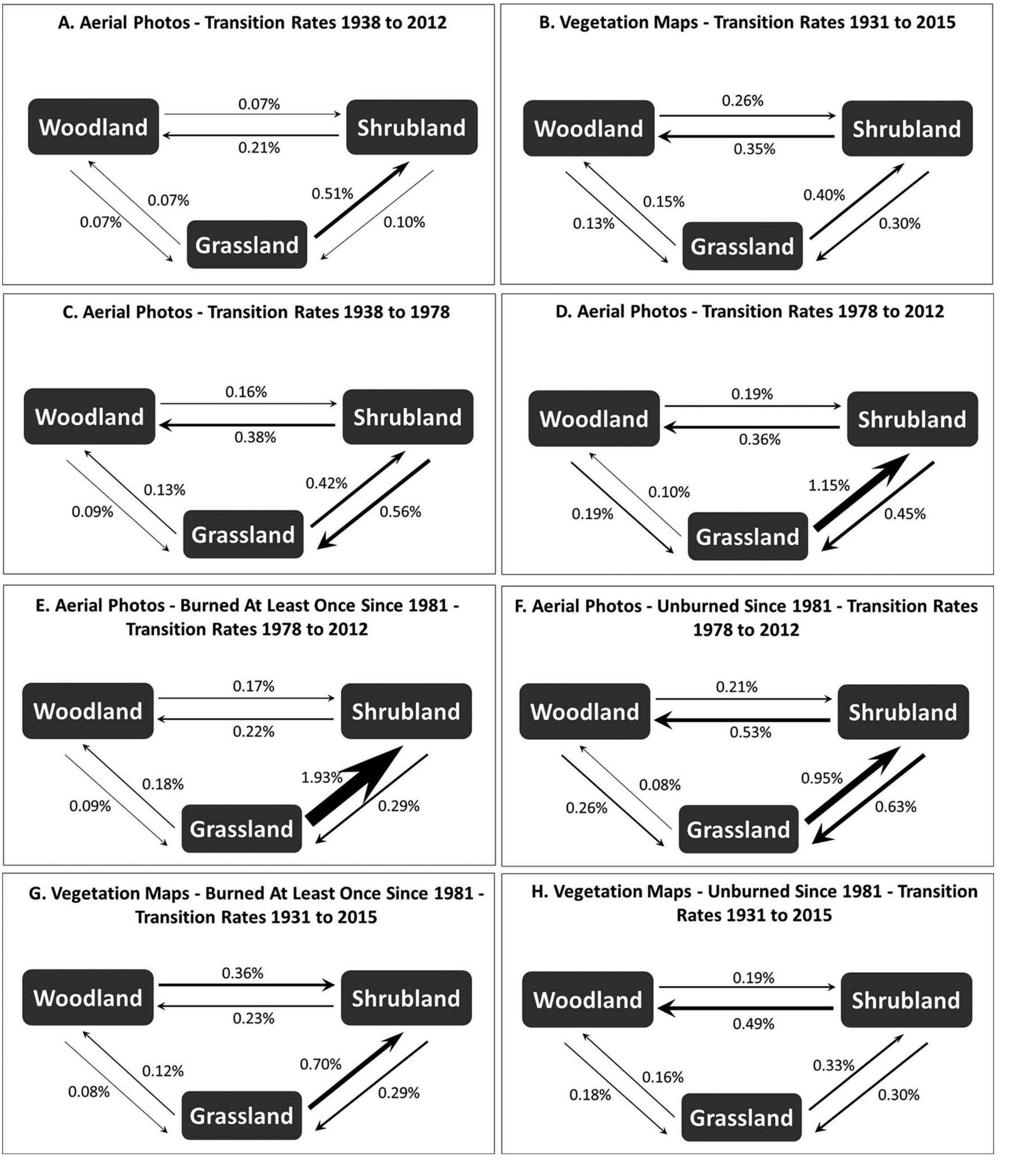

FIG. 8. Annualized transition rates (%/year) between woodland, shrubland, and grassland. The transition rate from habitat type X to type Y was calculated as the percentage of sample points (aerial photos analysis) or raster cells (vegetation map analysis) that converted from X-type in earlier time point to Y-type in later time point divided by the total number of X-type sample points/raster cells in the earlier time point. Then this rate was annualized to facilitate comparisons between time periods of different length.

Wildfire suppression has also been linked to shrubland and woodland expansion in California (McBride and Heady 1968; Freudenberger et al. 1987; Keeley 2005; Hsu et al. 2012) and has been shown to reduce herbaceous species richness in coastal wetlands, due to buildup of litter and shading (Saler and Jules 2021). Our analysis comparing transition rates between burned and unburned areas of the Preserve suggests that shrubland-to-woodland transition happened relatively more often in unburned areas than it did in burned areas.

This is consistent with other studies in the Santa Barbara region, including Sousa et al. (2022), which quantified changes and potential drivers in oak cover across the Preserve from 1982–2020. Research on the Burton Mesa in Santa Barbara County demonstrated that Coast Live Oak canopy cover increases with time since the last fire (Davis et al. 1988) and that the presence of shrubs is associated with increased seedling survival of Coast Live Oak (Callaway and D'Antonio 1991; Brennan et al. 2018). The association between fire and oak trees is also evident in historical pollen records. These records indicate that the amount of oak pollen in the Santa Barbara region remained stable from the 1400s to 1870, when it began to steadily increase, suggesting an increase in oak cover and/or density (Mensing 1998). Mensing (1998) speculates that this is a result of a changing fire regime, because the shift coincides with European settlement in Santa Barbara. Prior to Spanish colonization, the native Chumash people frequently set fires to improve their harvests; today, fire suppression starting around 1910 (Cermak 2005) is a common practice.

While our finding that lack of fire is associated with greater shrubland-to-woodland transition in southern California's coastal vegetation is expected and consistent with other studies (McBride and Heady 1968; Callaway and Davis 1993; Zavaleta and Kettley 2006), our results for fire effects on grassland-to-shrubland transition are less so. Our analysis comparing transition rates between burned and unburned areas of the Preserve suggests that the grassland-to-shrubland transition happened relatively more often in burned areas of the Preserve than it did in unburned areas. This contrasts with a study at nearby Gaviota State Park, where grassland-to-shrubland transition was higher in unburned plots (Callaway and Davis 1993). One reason for this discrepancy could be that the fire record for the Dangermond Preserve is incomplete; it is possible that areas we identified as "unburned" have in fact burned, but these fires were not recorded in the FRAP database. The FRAP data is the most comprehensive record of fire history in California, with fires reported back to 1878; however, there are still limitations with the data record, including missing data or lost/damaged historical records (California Department of Forestry and Fire Protection 2017). Anecdotal records from ranchers who have worked at the Preserve for more than 50 years support the idea that there were more prescribed fire and shrubland clearing events (designed to reduce shrubland encroachment and maintain grazing land) than what is documented in FRAP and other land management data. Another potential explanation could be that the interval between fires at the Dangermond Preserve may have been relatively long. Some scrub and chaparral species present on the property are adapted to regenerate after fire, provided the fire return interval is not less than 20 years for chaparral or 10 years for sage scrub (Keeley et al. 2011). The relatively long fire return intervals on record for this area and the increase in chaparral extent is in contrast to extensive conversion of shrubland to non-native grasslands in southern California, which are associated with higher fire frequency (Zedler et al. 1983; Park & Jenerette 2019). Grassland-shrubland transition rates may also differ between areas burned by wildfire versus prescribed fire, considering that areas of the Preserve with prescribed burns may have been more subject to other shrubland clearing techniques or to livestock grazing. Future research into the fire history of the Preserve will likely improve our understanding of the vegetation changes documented here.

The increase in shrubland at the Preserve may have increased the potential for high intensity fire, especially in more xeric areas of the Preserve. Fuel sampling in the San Francisco Bay region found that *Baccharis*-dominated shrublands had surface fuels five times greater than oak and more than 10 times greater than grassland (Russell and McBride 2003). In addition, the presence of non-native grass species can be an important predictor for increased fire occurrence and frequency, potentially due to an increase in fuel loads and horizontal fuel continuity (Fusco et al. 2019). With climate change, the risk of high severity fire at the Preserve will continue to increase. A study of coastal southern California found that May–September clouds have become less common and have risen in altitude (Williams et al. 2018). This change in cloud patterns leads to more solar radiation reaching the surface, which in turn increases temperature and evaporative demand, leading to decreased fuel moisture. To date, climate change in this area has been measurable. Extractions of decadal historical climate from statewide maps (Thorne et al. 2015; Flint et al. 2013) for the Preserve show an increase of 1.7°C in the mean annual nighttime lows from the 1930s to the 2010s, stable mean annual daytime highs around 20°C, and a decrease in mean annual precipitation of 3 cm.

Our findings also have implications for biodiversity management. Grassland is an abundant habitat at the Preserve, covering 2,053 ha (5,074 acres) or 21% of the total area. Our results suggest that significant grassland habitats will convert to shrub and woodlands in the absence of active management. Grassland habitats harbor many species of conservation concern—a diverse group of plants, mammals, birds, reptiles, amphibians, and insects, including the federally endangered Gaviota Tarplant – *Deinandra increscens* (D.D.Keck) B.G.Baldwin subsp. *villosa* (Tanowitz) B.G.Baldwin; as well as California sensitive species like the American Badger (*Taxidea taxus*), Grasshopper Sparrow (*Ammodramus savannarum*), and Burrowing Owl (*Athene cunicularia*). Management of livestock grazing and prescribed fire have been shown to be effective tools for grassland management in California (e.g., D'Antonio et al. 2002; Gennet et al. 2017; Bartolome et al. 2014).

In summary, our study using two lines of evidence—aerial photographs and vegetation maps—proved to be a powerful system to detect change in vegetation at the Preserve. Namely, grassland extent has decreased since the 1930s, with grassland-to-shrubland and shrubland-to-woodland transitions being most common. These findings, taken with similar trends observed across the central coast (McBride and Heady 1968; Callaway and Davis 1993; Russell and McBride 2003; Keeley 2005; Hsu et al. 2012), increase the motivation for further work on restoration of native grassland species in this region. Furthermore, the fact that the vegetation changes we observed were coincident with decreases in grazing and prescribed fire points to the possibility of using active, adaptive management strategies such as strategic livestock grazing and prescribed fire as interventions to maintain grassland communities and to reduce risk of high severity fire, especially in light of a changing climate.

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