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CHANGES IN VEGETATION AND BIOLOGICAL SOIL CRUST COMMUNITIES ON SAND DUNES STABILIZING AFTER A CENTURY OF GRAZING ON SAN MIGUEL ISLAND, CHANNEL ISLANDS NATIONAL PARK, CALIFORNIA

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ABSTRACT.—San Miguel Island is the westernmost of the California Channel Islands and one of the windiest areas on the west coast of North America. The majority of the island is covered by coastal sand dunes, which were stripped of vegetation and subsequently mobilized due to droughts and sheep ranching during the late 19th century and early 20th century. Since the removal of grazing animals, vegetation and biological soil crusts have once again stabilized many of the island's dunes. In this study, historical aerial photographs and field surveys were used to develop a chronosequence of the pattern of change in vegetation communities and biological soil crust levels of development (LOD) along a gradient of dune stabilization. Historical aerial photographs from 1929, 1954, 1977, and 2009 were georeferenced and used to delineate changes in vegetation canopy cover and active (unvegetated) dune extent among 5 historical periods (pre-1929, 1929–1954, 1954–1977, 1977–2009, and 2009–2011). During fieldwork, vegetation and biological soil crust communities were mapped along transects distributed throughout San Miguel Island's central dune field on land forms that had stabilized during the 5 time periods of interest. Analyses in a geographic information system (GIS) quantified the pattern of changes that vegetation and biological soil crust communities have exhibited on the San Miguel Island dunes over the past 80 years. Results revealed that a continuing increase in total vegetation cover and a complex pattern of change in vegetation communities have taken place on the San Miguel Island dunes since the removal of grazing animals. The highly specialized native vascular vegetation (sea rocket, dunedelion, beach-bur, and locoweed) are the pioneer stabilizers of the dunes. This pioneer community is replaced in later stages by communities that are dominated by native shrubs (coastal goldenbush, silver lupine, coyote-brush, and giant coreopsis), with apparently overlapping or cyclical succession pathways. Many of the dunes that have been stabilized the longest (since before 1929) are dominated by exotic grasses. Stands of biological soil crusts (cyanobacteria) are found only on dunes where vascular vegetation is already present. Biological soil crusts are not found on dunes exhibiting a closed vascular plant canopy, which may indicate that the role of soil crusts in dune stabilization on the island is transitory. Particle-size analyses of soil samples from the study area reveal that higher biological soil crust LOD is positively correlated with increasing fine grain content. The findings indicate that changes in vegetation communities may be the most rapid at earlier and later stages of dune stabilization and that regular monitoring of dunes may help to identify the interactions between vegetation and soil crusts, as well as the potential transitions between native and exotic plant communities.

RESUMEN.—La Isla San Miguel es la más occidental de las Islas del Canal de California y una de las áreas más ventosas de la costa oeste de Norteamérica. La mayoría de la isla está cubierta por dunas de arena costera, desprovistas de vegetación, se movilizaron debido a las sequías y a la cría de ovejas durante finales del siglo XIX y principios del siglo XX. Desde la remoción de los animales de pastoreo, la vegetación y las cortezas de sedimentos biológicos han estabilizado una vez más muchas de las dunas de la isla. En este estudio, se utilizaron fotografías aéreas históricas y estudios de campo para desarrollar una cronosecuencia del patrón de cambio en las comunidades de vegetación y los niveles de desarrollo de la corteza de sedimentos biológicos (LOD, por sus siglas en inglés) junto con una gradación de la estabilización de la duna. Las fotografías aéreas históricas de 1929, 1954, 1977, y 2009 fueron georeferenciadas y se usaron para delinear la extensión de cambios en la cubierta de vegetación y en dunas activas (sin vegetación) entre los cinco períodos históricos (pre-1929, 1929–1954, 1954–1977, 1977–2009, y 2009–2011). Durante el trabajo de campo, las comunidades de vegetación y de corteza de sedimentos biológicos se mapearon a lo largo de los cortes transversales distribuidos a lo largo de las formas de campos de dunas centrales de la Isla San Miguel que se habían estabilizado durante los cinco períodos de interés. Los análisis en el sistema de información geográfica (SIG, por sus siglas en inglés) cuantificaron el patrón de cambios que las comunidades de vegetación y de cortezas de sedimentos biológicos han exhibido en las dunas de la Isla San Miguel durante los últimos 80 años. Los resultados revelaron que un aumento continuo en la cubierta total de vegetación y un patrón complejo de cambio en las comunidades vegetales han tenido lugar en las dunas de la Isla San Miguel desde la expulsión de animales de pastoreo. La vegetación vascular nativa altamente especializada (estrellita marina, diente de león, ambrosía y astrágalo) son los estabilizadores pioneros de las dunas. Esta comunidad pionera se sustituye en etapas posteriores por comunidades dominadas por arbustos nativos (arbusto dorado costero, lupina plateada, bacaris y coreopsis gigante), con caminos aparentemente superpuestos o en sucesión cíclica. Muchas de

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las dunas que han estado estabilizadas por más tiempo (desde antes de 1929) están dominadas por hierbas exóticas. Gradas de cortezas de sedimentos biológicos (cianobacterias) se encuentran únicamente en las dunas donde la vegetación vascular ya está presente y no se encuentra en dunas que exhiben una cubierta de plantas vasculares cerrada, lo cual puede indicar que su papel en la estabilización de la duna de la isla es transitoria. Los análisis de tamaño de partículas de las muestras de terreno, del área de estudio, revelan que los niveles de desarrollo de corteza de sedimentos biológicos más altos están positivamente correlacionados con los contenidos crecientes de grano fino. Los hallazgos indican que los cambios en las comunidades de vegetación podrían ser más rápidos en etapas tempranas y más tardías de estabilización de las dunas, y que la monitorización regular de las dunas podría ayudar a identificar las interacciones entre la vegetación y las cortezas de sedimentos, así como las potenciales transiciones entre comunidades de plantas nativas y exóticas.

In coastal sand dune ecosystems, interactions among geology, climate, and vegetation create naturally dynamic environments (Martinez et al. 2004, Miller et al. 2010). Dunes are found in nearly all latitudes and cover ecological habitats from deserts to tropical rain forests (Snead 1972). Many coastal dune ecosystems have been greatly modified by anthropogenic disturbances (Martinez et al. 2004), which often alter vegetation communities and subsequently influence geomorphology if the substrate is exposed to wind and water erosion. Because of natural resource exploitation, demographic expansion, industrial growth, and recreation, most coastal dune systems are in a state of continuous disturbance. As a result, the manner in which pathways of physical (geomorphic) change and ecological (vegetative) change interact may be observed, monitored, and, ideally, managed to facilitate conservation and recovery efforts.

Coastal sand dunes are considered one of the best environments in which to study primary ecological succession, defined as the establishment of plants on land not previously vegetated (Barbour et al. 1998), because the shifting surface of sand provides a substrate not previously colonized with vegetation (Doing 1985, Burrows 1990, Lichter 1998, Ujházy et al. 2011). In coastal dune environments, the pioneer vegetation community must be highly specialized to survive the harsh environment presented by the unstable surface and low moisture-holding capacity of the sand. Once the pioneer community is established, the dune surface is stabilized and the process of soil development is initiated. In addition, the organic-matter content, pH, moisture-holding capacity, and nutrient composition of the soils are altered (Barbour et al. 1998). These changes in soil properties and microclimate make the environment more hospitable for other plant species and allow rapid changes in vegetation communities over time (Kumler 1969). From there, multiple trajectories for succession are possible, including single or multiple pathways that can be parallel, convergent, divergent, or cyclic, or that can form complex networks (Walker and del Moral 2003).

Vascular vegetation is not the only facilitator of early stages of sand dune stabilization. In areas where soil surface disturbance has taken place, early colonizers may include a biological soil crust community consisting of cyanobacteria, mosses, and lichens (Anderson and Rushforth 1976, Johansen and Rushforth 1985, Harper and Marble 1988, Belnap et al. 2001). In some semiarid and arid ecosystems, biological soil crusts can represent up to 70% of the living ground cover (Belnap 1994). Biological soil crusts can strongly influence vascular vegetation development by modifying soils in ways that affect higher-order plants. Examples of such effects include increasing surface roughness, fixing nitrogen, contributing nutrients, facilitating seedling germination, and improving soil-plant-water relations (Belnap 1994, Belnap et al. 2001). Prior to the mid-20th century, denudation of vegetation on coastal and desert dunes in Israel occurred due to animal grazing and other human activity, but the dunes have been stabilizing since 1948, when Bedouin pastoral nomads were evicted from their habitats on the Israeli side of the newly defined Israel–Egypt border (Meir and Tsoar 1996). Several studies have found that an increase in vegetation cover and development of biological soil crusts on these dunes resulted in an increase in surface roughness that facilitates the trapping of fine-grained silt and clay particles (Danin and Yaalon 1982, Tsoar and Moller 1986, Danin et al. 1989, Hesp 1991, Leys and Eldridge 1998, Levin et al. 2007). These fines increase a dune's water-holding capacity, facilitate higher plant densities, and enable further vegetation succession. Cyanobacteria are the most common

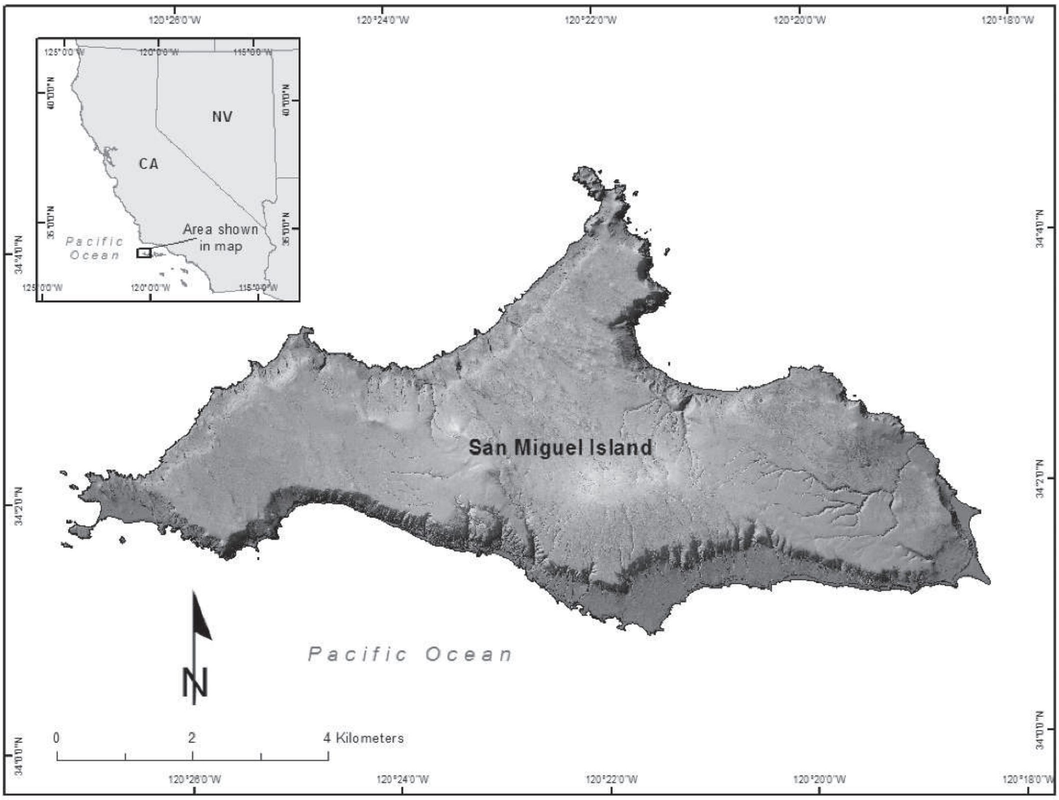

Fig. 1. San Miguel Island location map.

biological soil crust component on these dunes and are accompanied by soil algae, mosses, and lichens (Danin et al. 1989).

San Miguel Island, which is off the coast of southern California (Fig. 1), presents an unusual opportunity to study coastal sand dune stabilization and the changes in biological soil crust and vegetation on a landscape that is currently exposed to minimal human and animal disturbance after decades of significant disturbance from grazing. Similar to the dune systems studied in Israel, San Miguel Island was heavily grazed by livestock prior to the mid-1900s. However, in contrast to the situation in Israel, minimal subsequent disturbance has occurred on the island since grazing ceased completely in the 1960s. As part of Channel Islands National Park, San Miguel Island is protected by land management practices that have removed all nonnative herbivores and restricted human activity, allowing for recovery of vegetation and biological soil crusts. These conditions, combined with an extensive aerial photograph archive and low biodiversity, make San Miguel Island an appropriate site to conduct a chronosequence assessment (Walker et al. 2010) of the changes in vegetation communities and biological soil crust development following disturbance.

In this study, a chronosequence approach was used to evaluate the pattern of change in vegetation communities and biological soil crusts over an 80-year time span as the San Miguel Island dunes stabilized after experiencing significant disturbance from livestock grazing. The following questions were addressed: (1) How have the extent of active dunes and vegetation cover changed in the central dune field over the past 80 years? (2) Which vegetation communities are present on dunes representing 5 post-grazing historical periods (prior to 1929, 1929–1954, 1954–1977, 1977–2009, and 2009–present)? (3) Do the presence and level of development (LOD) of biological soil crust vary among the 5 time periods? (4) Is the amount and LOD of biological soil crust related to the percent cover of vegetation or the type of vegetation community present? (5) Is the amount and LOD of biological soil crust related to the percentage of fine particles in the soil?

STUDY AREA

Located approximately 44 km southwest from the coast of Santa Barbara, California, San Miguel Island is the westernmost of the Northern Channel Islands (Fig. 1). At its farthest extent, the island measures 13 km long and 6 km wide. San Miguel Island lies exposed to the full force of the predominantly northwest winds and the cool California current, which sweeps south of Point Conception, making the island one of the windiest and foggiest areas on the west coast of North America. The climate of San Miguel Island follows a maritime Mediterranean pattern that is similar to the rest of coastal California, bringing wet winters, dry summers, and mild temperatures year-round (Western Regional Climate Center 2012).

Nearly two-thirds of the island is covered by distinctively white coastal sand dunes. The white color results from a high calcium carbonate ($CaCO_3$) content, which composes approximately 40% of the sand (Johnson 1972, Muhs et al. 2009). Previous studies found that the dunes accumulated in 3 stages that correspond to glacial periods during the Pleistocene when sea level was low (Johnson 1972, Muhs 1992, Muhs et al. 2009): (1) the lowered sea level exposed the carbonate-rich sand, which is largely composed of the skeletal remains of sea-dwelling organisms; (2) the sands were then carried by the wind and deposited as dunes; and (3) the source of the sand was cut off with the sea-level rise that accompanied the end of a glacial period. With no new supplies of sand, the dunes may undergo stabilization by vegetation and weak cementation to eolianite. According to this conceptual model, dunes on San Miguel Island should have been stable since the close of the last glacial period and the beginning of the Holocene, approximately 10,000 years before present. However, postglacial sea-level rise, coastal erosion, human activities (predominantly livestock grazing), and lightening-induced fires have reactivated some of these dunes in both prehistoric and historic time (Johnson 1980, Erlandson et al. 2005).

At present, San Miguel Island contains 3 dune areas, designated informally as the Western Dune Field, the Central Dune Field, and the Eastern Dune Field. The main landforms are linear dunes, with the long axes oriented northwest to southeast, parallel to the direction of the prevailing wind. The westernmost part of the Western Dune Field consists primarily of thin eolian sand over a laminar petrocalcic horizon that developed in Pleistocene eolianite (often referred to as "caliche" in the literature). The easternmost part of the Western Dune Field consists of vegetated linear dunes oriented northwest to southeast. The Eastern Dune Field is still very active in places and is currently fed by sand from the beach at Cuyler Harbor. The Central Dune Field exhibits the most drastic changes in active dune extent based on the aerial photograph record. These dunes are fed to some extent by sand from the beach at Simonton Cove, but less so than is the case in the Eastern Dune Field. The Central Dune Field was selected as the sampling location for the field investigation because of the pronounced revegetation of formerly active sand in the past 80 years, following a period of significant disturbance.

GRAZING HISTORY

The combination of drought events and overintensive grazing has had significant negative impacts on vegetation communities and has affected dune dynamics on San Miguel Island since the mid-1800s. Historical accounts from the 1850s describe San Miguel Island as being covered almost entirely with grass and shrubs (Alden 1852, Greenwell 1857, Davidson 1858 reviewed *in* Johnson 1980). Sheep ranching began on the island sometime around 1850, when ranchers from the California mainland discovered that San Miguel Island offered an abundant food source for their livestock in a geographic setting that would not require herding. By 1863, the island held some 6000 sheep, 125 head of cattle, and 25 horses (Santa Barbara County Records Office, Miscellaneous Book A, pp. 313–314). With a total area of only 40.5 km^2, the collective number of animals (about 6200) was likely well beyond the island's carrying capacity. In 1863–1864, a severe drought affected southern California and lasted for nearly 3 years, starving almost 80% of the livestock on San Miguel

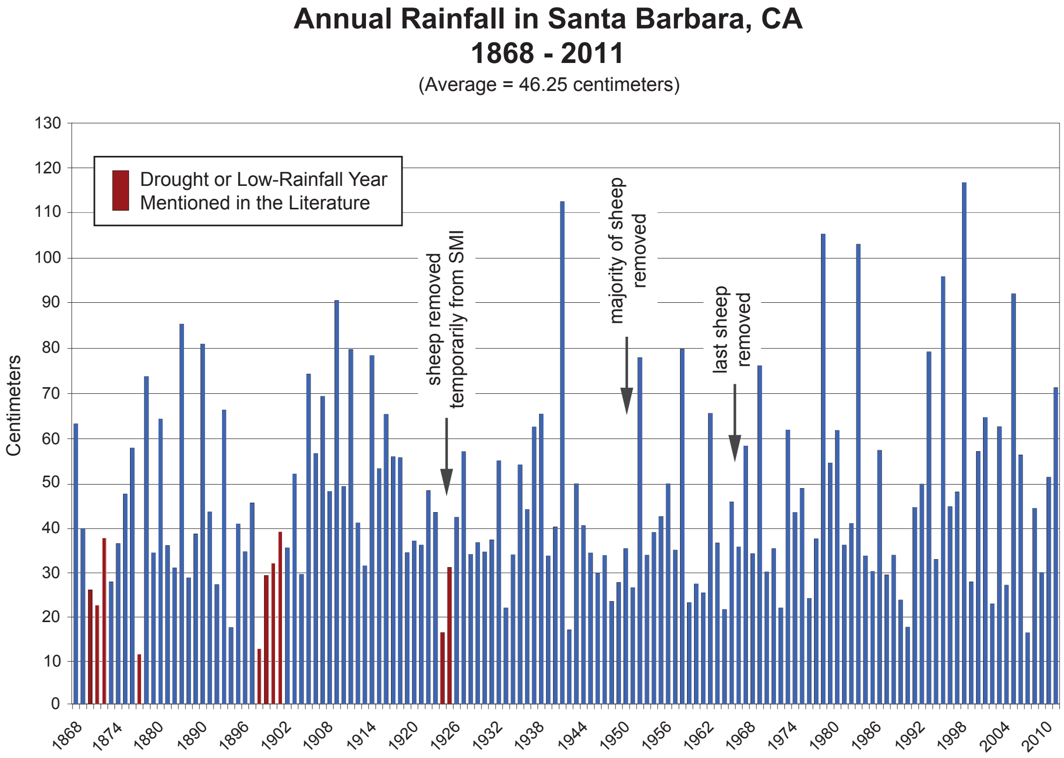

Fig. 2. Annual precipitation record from Santa Barbara, California, 1868–2011. Redrawn from a graph obtained from the county of Santa Barbara Online (2012). Drought and low-rainfall years mentioned in the literature as contributing factors to vegetation denudation on San Miguel Island are shown in red.

Island (Ellison 1937). During this drought, the majority of the available vegetation on the island was consumed, often including the roots. Additional droughts struck coastal California in 1870–1872, 1877, and 1897–1900 (Fig. 2). In the decades after each great drought, much of San Miguel Island was covered with drifting sand and blowing soil (Johnson 1980, Erlandson et al. 2005). During the low-rainfall years of 1923–1924, all livestock were removed from the island because of a lack of food (Johnson 1980), but sheep were later brought back (year unknown). The majority of the sheep were finally removed in 1950, although limited sheep ranching continued until July 1966 (Roberts 1991), when the last sheep were removed, ending over a century of livestock grazing (Roberts 1991).

Livestock ranching had a pronounced effect on the geomorphology of San Miguel Island that is evident in the present-day landscape. Grazing and trampling removed vegetation, allowing soils to be easily eroded and dunes to be reactivated by the strong winds. In many areas, the soil was eroded down to the impermeable petrocalcic horizon. Severe water erosion cut deep ravines that now dissect large areas of the inland landscape and caused gullying along the periphery of the entire island (Johnson 1980). To illustrate how the past disturbance, removal of livestock, and subsequent recovery of the vegetation altered the landscape of San Miguel Island, Johnson (1972, 1980) compiled hand-drawn maps dating from 1871, 1893, and 1910, and aerial photograph mosaics from 1929 through 1972. These aerial photographs show a progressive recovery of dune vegetation that has been reducing the extent of the active dunes since 1929, especially after the majority of sheep were removed in 1950.

Dune Vegetation Communities on San Miguel Island

Vascular vegetation on San Miguel Island is dominated by native species. About 220 different plants are found on the island, including

TABLE 1. Dominant species in San Miguel Island dune vegetation communities.

Vegetation community	Latin name	Common name
Pioneer Coastal Dune Scrub	*Cakile maritima*	sea-rocket
	Malacothrix incana	dunedelion
	Ambrosia chamissonis	beach-bur
	Astragalus traskiae	locoweed
	Abronia umbellata	beach sand-verbena
	Carpobrotus sp.	iceplant or sea fig
Mixed Coastal Dune Scrub	*Cakile maritima*	sea-rocket
	Malacothrix incana	dunedelion
	Ambrosia chamissonis	beach-bur
	Astragalus traskiae	locoweed
	Abronia umbellata	beach sand-verbena
	Carpobrotus sp.	iceplant or sea fig
	Calystegia macrostegia	island morning-glory
	Erigeron glaucus	seaside daisy
	Camissonia cheiranthifolia	beach primrose
Mixed Goldenbush Scrub	*Isocoma menziesii*	coastal goldenbush
	Calystegia macrostegia	island morning-glory
	Bromus sp.	ripgut brome, soft chess
	Astragalus traskiae	locoweed
	Carpobrotus sp.	iceplant or sea fig
Lupine Scrub	*Lupinus albifrons*	silver lupine
Coyote-Brush Scrub	*Baccharis pilularis*	coyote brush
	Bromus sp.	ripgut brome, soft chess
	Lupinus albifrons	silver lupine
	Carpobrotus sp.	iceplant or sea fig
Coreopsis Scrub	*Leptosyne gigantea*	giant coreopsis
Grassland	*Avena* sp.	slender wild oats
	Bromus sp.	ripgut brome, soft chess
Iceplant Carpet	*Carpobrotus* sp.	iceplant or sea fig
Caliche Scrub	*Isocoma menziesii*	coastal goldenbush
	Achillea millefolium	yarrow
	Carpobrotus sp.	iceplant or sea fig

island endemics, other natives, and introduced plants (Junak et al. 2007). Currently, there are no large trees or shrubs on San Miguel Island, but beach and coastal dune vegetation communities are widespread. The vegetation communities present on the San Miguel Island dunes are similar to a subset of the communities described for San Nicolas Island by Junak (2008). San Nicolas Island, another of the California Channel Islands, is very similar to San Miguel Island in climate, vegetation communities, landforms, and history of dune vegetation disturbance by grazing (Vedder and Norris 1963, Junak 2008).

Eight of the San Nicolas plant communities described by Junak (2008) were identified on San Miguel Island. These include the southern beach and coastal dune scrub, valley and foothill grassland, annual iceplant, caliche scrub, mixed goldenbush scrub, coyote-brush scrub, lupine scrub, and coreopsis scrub communities. However, Junak's classification was modified in this study by recognizing that there are some differences in codominant species and associates (Table 1). For example, the "valley and foothill grassland" community on San Nicolas Island (Junak 2008) contains species that were not identified on San Miguel Island. For this study, the grass-dominated community was classified simply as "grassland." Junak's "southern beach and coastal dune scrub" community was broken into 2 communities for this study—"pioneer coastal dune scrub" and "mixed coastal dune scrub"—to represent 2 distinct communities apparent during the early stages of succession within the coastal dune scrub community on San Miguel Island. Finally, the iceplant-dominated community identified on San Nicolas Island and classified as "annual iceplant" by Junak (2008) is composed of a different species than the iceplant found on San Miguel Island, which is commonly known as "sea fig." For this study, the community was classified as "iceplant carpet," which is a community name that has been used previously for San Miguel Island (Junak et al. 2007).

Table 1 lists the vegetation communities and dominant species used for identification within the study area. Detailed descriptions of the plant communities present on San Miguel Island can be found in Zellman (2012).

Invasive plant species comprise over 25% of the known plants within Channel Islands National Park (Junak et al. 2007). The primary invasive taxa on San Miguel Island are 2 genera of iceplant (*Carpobrotus* sp. and *Mesembryanthemum* sp.), both of which are creeping succulent plants native to South Africa. They were introduced to California in the early 1900s to aid in slope stabilization. These plants pose a serious ecological problem because they form vast monospecific zones, lower biodiversity, and compete directly with native plant species for nutrients, water, light, and space (D'Antonio 1993).

METHODS

Analysis of Historical Aerial Photographs

This study extends the aerial photograph record presented by Johnson (1980) an additional 37 years, to 2009 (Fig. 3). Although not all of the images Johnson used were available, aerial photographs were acquired from the University of California Santa Barbara (UCSB) Map Library and the U.S. Geological Survey (USGS) archives from the years 1929, 1940, 1954, 1960, 1967, 1977, 1983, 1994, and 2009. With the exception of the 2009 Digital Orthophoto Quarter Quad (DOQQ), all of the images were scanned from hard-copy aerial photographs and were not orthorectified or georeferenced. For this study, the 1929, 1954, and 1977 aerial photographs were selected to represent a chronosequence for analysis of active dune extents and patterns of vegetation and biological soil crust over intervals of approximately 25–30 years. The most recent high-resolution aerial photographs of the island, taken in 2009, were used to determine the approximate present-day extent of active dunes and the change in extent of active dunes since 1977. Thus, the chronosequence represents 5 historical postgrazing periods: pre-1929, 1929–1954, 1954–1977, 1977–2009, and 2009–2011.

To georeference the historical aerial photographs, the 2009 DOQQ and Light Detection and Ranging (LiDAR) data collected by NOAA in 2010 were loaded into the Environmental Systems Research Institute's (ESRI) ArcGIS software to serve as base images. Many geologic and geographic features on the island were visible on both the historical photographs and the 2009 DOQQ or on a hillshade generated from the LiDAR imagery. These features were used as control points for georeferencing the historical aerial photographs and rectifying them as accurately as possible to a common reference map projection, given that the scale and resolution of the photographs were different for each date (Table 2). The georeferenced images were used in ArcGIS to digitize the extent of active sand dunes (defined as areas that had the characteristically white surface color of the sand and <10% vegetation canopy cover) from the 1929, 1954, 1977, and 2009 aerial photographs. Beaches were included in the active dune extents because they supply sand to the dunes and are therefore considered part of the active dune system. A shapefile representing the current shoreline of San Miguel Island was generated from Interferometric Synthetic Aperture Radar (IfSAR) data collected in 2003. Polygons representing the active dune extents for the 1929, 1954, 1977, and 2009 images were layered in ArcGIS to quantify and display the change in active dune extent between 1929, 1954, 1977, and 2009 (Fig. 4).

Field Surveys of Vegetation and Biological Soil Crusts

Sites for field investigation were identified in ArcGIS using the historical active dune extents for each of the 5 time periods. Site selection was subjective and intended to represent the range of conditions present on the San Miguel Island dunes. Thirty locations for field survey transects were selected throughout the Central Dune Field and were distributed to ensure that multiple transect lines covered each of the map units of interest: (1) dunes that are presently active; (2) dunes that stabilized between 1977 and 2009; (3) dunes that stabilized between 1954 and 1977; (4) dunes that stabilized between 1929 and 1954; and (5) areas outside of the dune fields that were never active over the course of the aerial photograph record (Fig. 4). The 200-m sampling transects were oriented perpendicular to the long axes of the linear dunes (Fig. 4). All field measurements were made between 1 August and 10 August 2011.

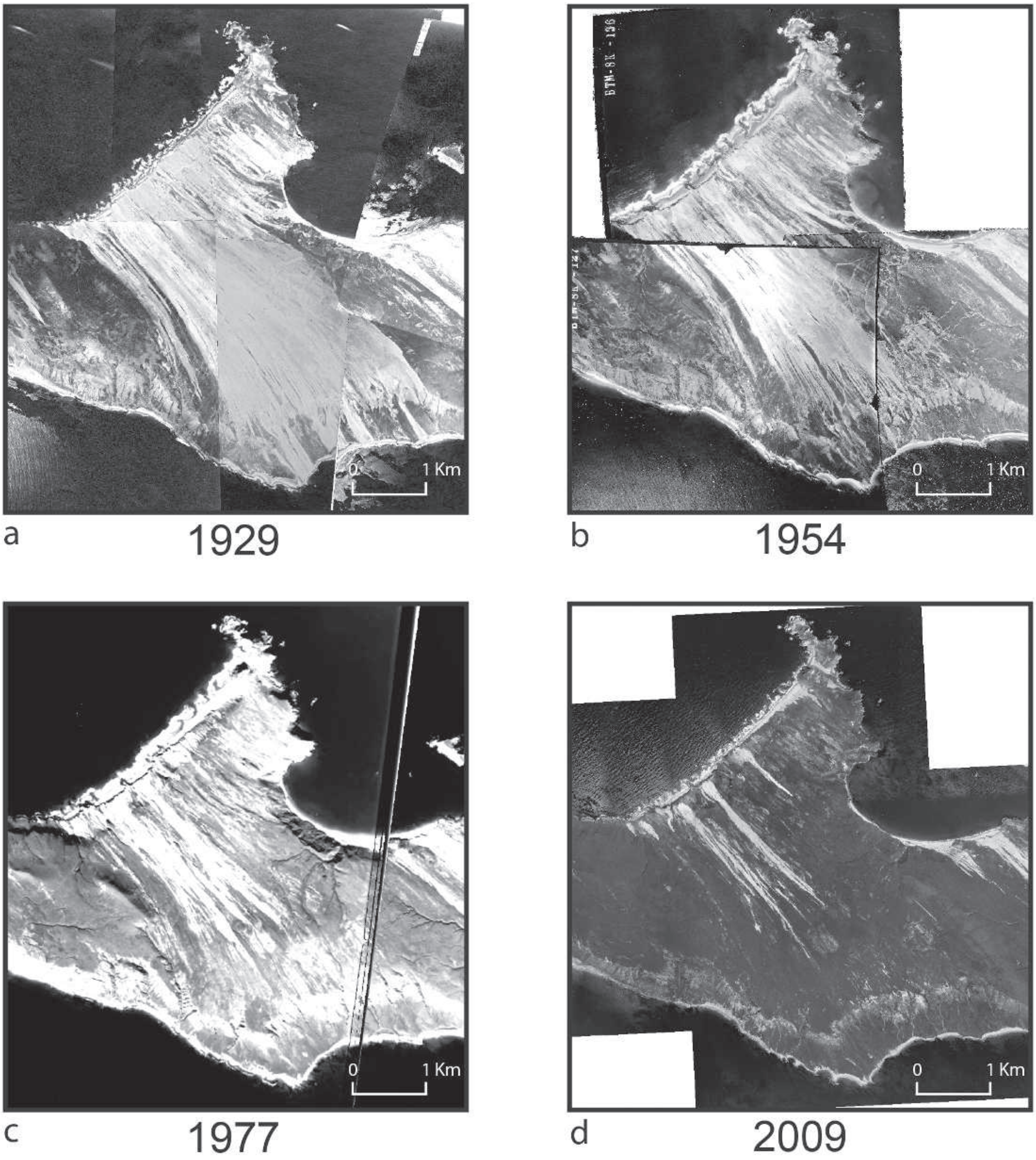

Fig. 3. Aerial photographs of the Central Dune Field: **a,** 1929; **b,** 1954; **c,** 1977; **d,** 2009.

TABLE 2. Aerial photograph date of acquisition and scale.

Year of acquisition	Day-month of acquisition	Resolution or scale
1929	1-Jun	1:18,000
1954	13-Mar	1:20,000
1977	14-Mar	1:65,117
2009	Unknown	1 ft.

Along each 200-m transect, the vegetation communities were measured using a modified version of the line-intercept method described by Canfield (1941). Typically, this method is used for determining the percent cover of each plant species within one vegetation community. Because species-level sampling was beyond the scope of this study, the line-intercept method was modified to measure the length of each vegetation community along the transect

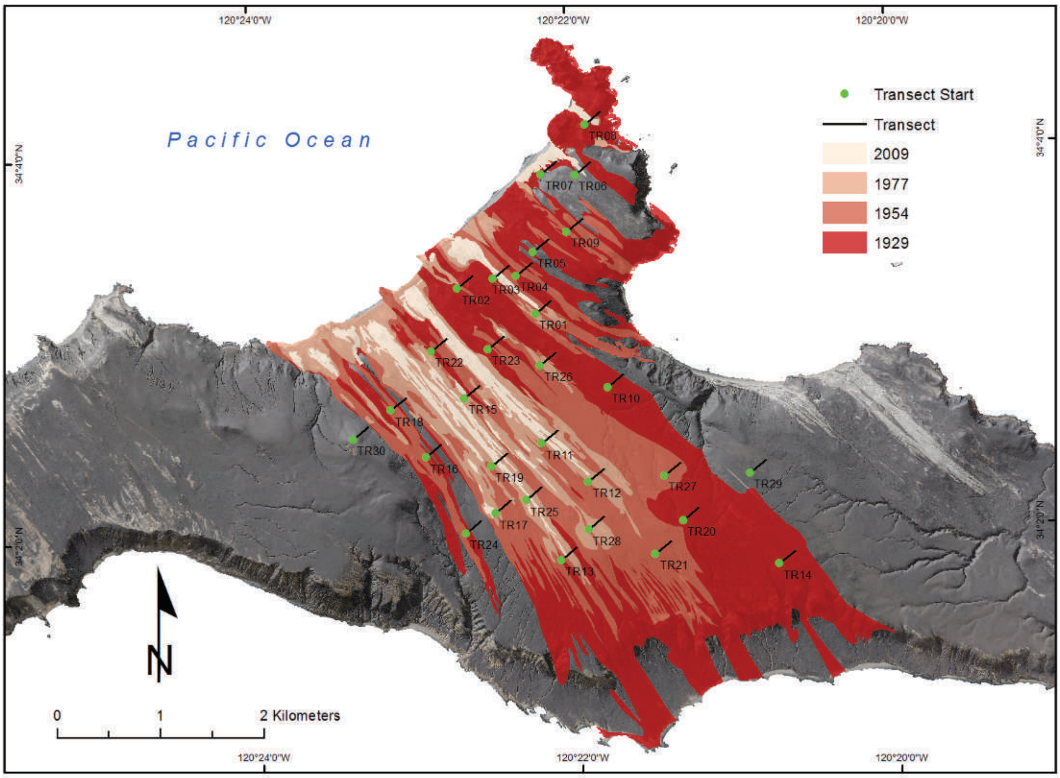

Fig. 4. Transect locations and historical active dune extent polygons in the Central Dune Field (1929–2009). Shading indicates areas of active dunes in the respective aerial photograph.

line. Each vegetation community was identified based on Junak's (2008) vegetation community classifications for San Nicolas Island (described above; Table 1). The following information was recorded along each transect: the distance covered by each vegetation community along the transect line, the percentage of ground covered by vascular vegetation within that community type (e.g., coyote-brush scrub was present along 20 m of a transect with 80% cover on average within that section), the distance along the transect covered by bare ground (<10% vegetation), if present, and a simple description of the soil color and texture (e.g., light, sandy soil; dark, fine-grained soil; presence of a petrocalcic horizon; etc.).

When a stand (patch) of biological soil crust was encountered along each transect, the biological soil crust type (cyanobacteria, moss, lichen) and the diameter of the soil crust stand were recorded. Each biological soil crust was examined and assigned an LOD classification (Fig. 5). The classifications were based on Belnap et al.'s (2008) LOD index for the visual assessment of cyanobacterially dominated biological soil crust development and soil surface stability. Belnap et al. recognize 6 LOD classes, based on color (lightness or darkness), that cover the range of development of cyanobacterially dominated biological soil crusts found in southeastern Utah, USA. In this study, the 6 LOD classes were modified to represent the range of biological soil crust LODs found on San Miguel Island (Fig. 5): class 1 represents the lightest color of cyanobacteria stands, and class 6 represents the darkest color of cyanobacteria stands. The classes also represent increasing surface roughness with higher LOD. Samples of soil supporting biological soil crust development were also collected from each patch for soil particle size analysis in the laboratory. Because only the surface layer of soil containing biological soil crusts was of interest to this study, a spot sampling technique was employed. Care was taken to sample only the soil attached to, and directly underneath, the

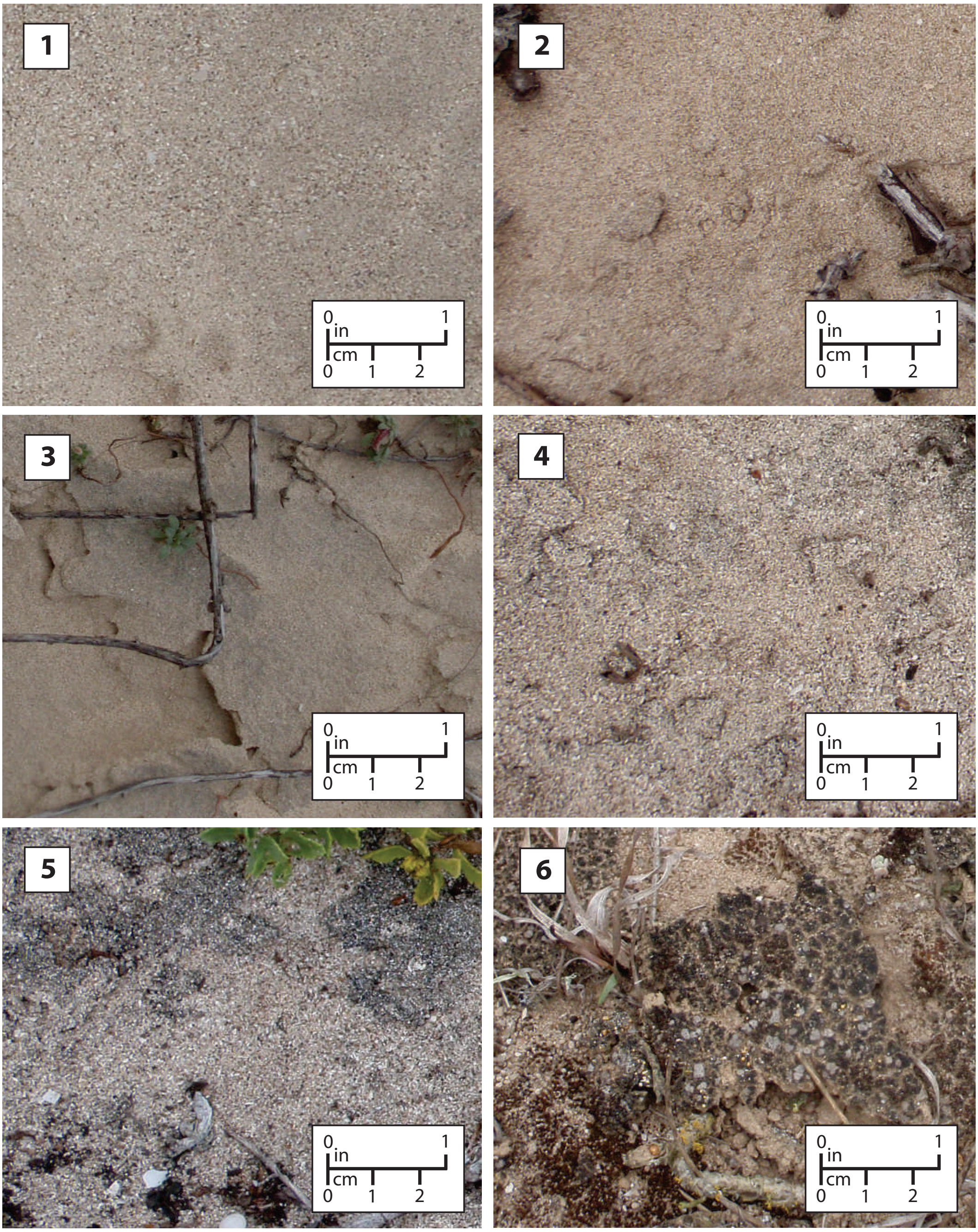

Fig. 5. San Miguel Island Biological Soil Crust Development Index. Classifications were based on Belnap et al.'s (2008) LOD index for the visual assessment of cyanobacterially dominated biological soil crust development and soil surface stability. Six LOD classes are shown, based on color (lightness or darkness). These LOD classes cover the range of development of cyanobacterially dominated biological soil crusts found on San Miguel Island. Class 1 represents the lightest color of cyanobacteria stands, and class 6 represents the darkest cyanobacteria-dominated areas. The classes also represent increasing surface roughness with higher LOD.

biological soil crust by using a masonry trowel to "skim" the surface of the dune. At least 50 g of soil was collected at each sample location.

Spatial Data Analysis

To quantify the proportion of each vegetation community present in each of the 5 time periods examined, spatial analysis was performed using ArcGIS. Lines representing each survey transect were created in ArcGIS. The lines were then converted to a series of points spaced 1 m apart and covering the length of each transect. Each point was assigned the data that were collected in the field for the vegetation community and biological soil crust development at that location. Using the GIS polygons of the active dune extents, we also classified each point as representing the time period during which the dune appears stable (i.e., on a dune that had stabilized before 1929, between 1929 and 1954, between 1954 and 1977, or between 2009 and 2011). Vegetation community boundaries are "fuzzy" by nature, and some spatial error was introduced during the georeferencing of the historical aerial photographs, given their different original resolutions and projections. To minimize this source of error, a 10-m buffer was applied to both sides of the dune-extent boundaries representing each of the 5 time periods. Any transect sample points that had fallen within the buffer area were removed (Appendix B in Zellman 2012). The final sample size of transect points representing dunes at each of the 5 periods was 726 points for dunes that stabilized before 1929; 1496 for the period 1929–1954; 1100 for the period 1954–1977; 568 for the period 1977–2009; and 175 for 2009–2011.

For each of the 5 time periods, we calculated the average proportion of each vegetation community type present and the average proportion of bare ground (patches of exposed sand or soil that were between areas covered by vegetation communities). The percentage of exotic communities present in each period was also calculated. Finally, the average percent cover of vegetation for dunes across all community types in each of the 5 time periods was compared. We identified all transect sections in which vegetation was present and calculated the average and range of all the cover percentages recorded for those sections for each of the 5 time periods.

Soil Particle Size Analysis

Particle size analyses were conducted to test the relationship between biological soil crust LOD and particle size of the soil that the crusts bind. Thirty samples consisting of a subset from each biological soil crust LOD were randomly selected for analysis.

PRETREATMENT AND DISPERSION.—The first step in the mechanical pretreatment of the San Miguel Island samples was to follow standard protocol for disaggregation of unconsolidated sediments as outlined in Folk (1974). The samples were placed into a mortar and gently disaggregated with a rubber cork–tipped pestle. The second step was to run each sample through a 1.0-mm sieve to remove large organic fragments, such as sticks and grass. The remainder of organic material was then removed through chemical treatment by treating each sample with a 30% hydrogen peroxide (H_2O_2) solution. Each sample was placed into a beaker and approximately 100 mL of hydrogen peroxide was added. Additional hydrogen peroxide was added as needed until all of the organic matter within the sample was consumed and the solution no longer displayed visible signs of reaction. This process took several days for samples with lower levels of biological soil crust development (LOD 1–2), approximately one month for samples with middle LODs (LOD 3–4), and nearly 2 months for samples with higher LODs (LOD 5–6).

Once the organic material in each sample was destroyed, the samples were washed into centrifuge containers by using distilled water. The samples were then spun in a centrifuge at 2500 RPM for 15 min to separate the soil from the distilled water and were then decanted. Next, 25 mL of sodium hexametaphosphate, $Na(PO_3)_6$, was added to each sample to disperse clastic soil particles. Sodium hexametaphosphate was chosen because it is particularly effective for dispersing calcareous soils without the prior removal of alkaline earth carbonates (Day 1965). Dispersion requires that the particles be separated by mechanical shearing action of turbulent mixing; therefore, each sample was placed in an ultrasonic bath for 15 min, and then allowed to sit in the sodium hexametaphosphate solution overnight. The samples were placed again in the ultrasonic bath for an additional 15 min the next day, just prior to sieving.

SIEVING.—The wet-sieving technique described by Day (1965) was employed to separate the sand and fine-grained particles. A 53-μm sieve was used to separate the coarse silt from the sand particles. A 38-μm sieve was placed below that to separate the coarse silt from the fine silt and clay particles. Samples were carefully sieved with distilled water until a visibly complete separation of the coarse and fine grains was achieved.

The fractions of sample collected in each sieve were carefully washed into labeled and preweighed Teflon beakers, which were then placed in a laboratory oven to dry overnight at 100 °C. The ultrafine particles and water with dispersant that collected in the beaker placed below the sieves were carefully washed into containers, which were then placed back into the centrifuge at 2500 RPM to once again separate the fine grains from suspension. The supernatant solution containing sodium hexametaphosphate was then poured off, and the sample was washed 3 times with distilled water to remove the dispersant. This fraction of the sample was carefully washed into a Teflon beaker, which was then placed into the laboratory oven to dry overnight at 100 °C.

Once dry, each fraction of sample was weighed in a beaker, and the weight of the beaker was subtracted to obtain the weight of each sample fraction (sand, coarse silts, and fine silts/clay). Each sample fraction weight was then divided by the total weight of the treated sample to determine the percentage of each particle-size category. The percentage of organic matter was also determined by subtracting the total weight of the treated sample from the initial sample weight and dividing the difference by the initial sample weight.

RESULTS

Spatial and Temporal Analysis of Active Dune Extents

The extent of active dunes (<10% vegetation cover) in the Central Dune Field has changed markedly since 1929. In 1929, approximately 12.83 km^2 of the Central Dune Field was covered in active dunes. In 1954, the active dunes covered about 6.21 km^2, and by 1977 the area of active dunes was reduced to 2.67 km^2. In 2009, the extent of active dunes in the Central Dune Field was approximately 0.91 km^2. These data indicate that the extent of active dunes has decreased by more than 50% approximately every 25 years since the start of the aerial photograph record. Between 1929 and 1954, 52% of the previously active dunes in the Central Dune Field stabilized with vegetation. By 1977, 57% of the dunes that were active in 1954 had stabilized. Between 1977 and 2009, 65% of the remaining dunes stabilized with vegetation.

Patterns of Change in Vegetation Communities over Time

AREAS STABILIZED PRIOR TO 1929.—Areas that were vegetated as of 1929, based on the aerial photographic evidence, were either stabilized by 1929 after previous disturbance or were not affected as severely by previous disturbance (i.e., had never been active). Because no photographs prior to 1929 are known to exist, it is not possible to determine which of these scenarios is correct. The sections of the survey transects that were stabilized by 1929 are dominated by the exotic grassland community (43%; Table 3), composed primarily of annual *Avena* sp. (slender wild oats) and *Bromus* spp. (ripgut brome and soft chess). As of 2011, the average canopy cover within all vegetation community types is 94% (SD 13%). The grassland communities within this period of stabilization are found in association with both dark, fine-grained soils and grey, sandy soils (approximately 55% and 45% of the area surveyed, respectively).

DUNES STABILIZED BETWEEN 1929 AND 1954.—This time interval includes areas that appear active on the 1929 aerial photographs but that were vegetated by the time the 1954 aerial photographs were taken. The plant communities in areas that were stabilized between 1929 and 1954 are dominated by the native scrub communities (mixed goldenbush scrub—18%, lupine scrub—23%, coyotebrush scrub—24%, and coreopsis scrub—13%; Table 3). The average total vegetation canopy cover within all vegetation community types is 87% (SD 25%). These communities are all found growing on gray, sandy soil.

DUNES STABILIZED BETWEEN 1954 AND 1977.—This time interval includes areas that appear active on the 1954 aerial photographs but that were vegetated by the time the 1977 aerial photographs were taken. The plant communities in areas that were stabilized between 1954 and 1977 are dominated by the native

TABLE 3. Percent cover of vegetation communities along the 2011 survey transects by period of dune stabilization.

Time period	% Pioneer coastal dune scrub	% Mixed coastal dune scrub	% Mixed goldenbush scrub	% Lupine scrub	% Coyote-brush scrub	% Coreopsis scrub	% Caliche scrub	% Grassland	% Iceplant carpet	Total % exotic communities[a]	Average % canopy cover of all vegetation along transects
Pre-1929	0.00	0.00	1.38	11.57	16.53	24.93	0.00	43.39	2.20	45.59	93.78
1929–1954	0.00	4.41	18.46	22.68	24.48	12.51	7.96	0.00	9.50	9.50	86.77
1954–1977	0.00	10.36	8.45	21.18	32.55	18.27	3.18	5.27	0.74	6.00	86.06
1977–2009	0.00	0.00	7.95	22.44	50.71	11.31	6.35	0.00	1.24	1.24	80.83
2009–2011	65.14	3.43	0.00	0.00	0.00	0.00	3.43	0.00	3.43	3.43	25.43

[a] Sum of the percent iceplant carpet and grassland communities for each period of dune stabilization.

scrub communities (lupine scrub—21%, coyote-brush scrub—33%, and coreopsis scrub—18%; Table 3). The average canopy cover within all vegetation community types is 86% (SD 22%). These communities are all found growing on gray, sandy soil.

DUNES STABILIZED BETWEEN 1977 AND 2009.—This time interval includes areas that appear active on the 1977 aerial photographs but that were vegetated by the time the 2009 aerial photographs were taken. The plant communities in areas that were stabilized between 1977 and 2009 are dominated by coyote-brush scrub (51%; Table 3). The average canopy cover within all vegetation community types is 81% (SD 26%). These communities are all found growing on light to gray sandy soil.

DUNES ACTIVE IN 2009.—Areas that appear active in the 2009 aerial photograph were further classified in the field in 2011 into 2 types: dunes that started to stabilize since 2009 and had >10% vegetation cover present; and dunes that were still active with <10% vegetation cover and more than 90% exposed sand. In the areas that had started to stabilize since 2009, 75% of the area surveyed is covered with vegetation, and the average canopy cover of these communities is 25% (SD 32%). Vegetation is dominated by the pioneer coastal dune scrub community (65% of all plant communities present; Table 3). Both the active and stabilized dunes consisted of light, sandy soil.

Biological Soil Crust Development

Biological soil crust development was not visible on any of the active dunes that lacked vascular vegetation in 2011 (Table 4). Small stands (measuring <50 cm in diameter) of cyanobacteria LOD class 1–3 were observed on dunes in early stages of stabilization (since 2009) that exhibit sparse pioneer coastal dune scrub vegetation. These stands of cyanobacteria are present only on the soil near the base of the plants and at a relatively high frequency (34 of 100 total occurrences were recorded in this setting; Table 4). Over all 5 time periods, biological soil crusts were seen occasionally in the mixed goldenbush scrub, lupine scrub, coyote-brush scrub, and coreopsis scrub communities, with LOD ranging from class 1 to 6, but most commonly occurring in class 1 to 3. These stands diminish in size and occurrence as the percentage of vascular vegetation cover increases (Table 4). Areas classified as 100%

TABLE 4. Biological soil crust (BSC) occurrence, size, and level of development (LOD) by period of dune stabilization.

Time period	Years since stabilization	Active dune extent (km^2)	% area sampled representing this phase	Average % canopy cover of all vegetation along transects	Counts of BSC	Average patch size (cm)	LOD of BSC
Pre-1929	>83	Unknown	17.86	93.78	1	8	2
1929–1954	58–83	12.83	36.80	86.77	27	14	1, 2, 3, 4, 5
1954–1977	35–58	6.21	27.06	86.06	18	21	1, 2, 3, 5, 6
1977–2009	3–35	2.67	13.97	80.83	20	17	2, 3, 4, 5, 6
2009–2011 (veg)	0–3	0.00	3.34	25.43	34	42	1, 2, 3
2009–2011 (no veg)	0–3	0.91	1.10	0	0	N/A	N/A

vegetation cover show negligible biological soil crust development under the plants. The most consistently well-developed stands of biological soil crust grow within the caliche scrub community on the surface of the exhumed petrocalcic horizon and in areas outside of the stabilized dunes on dark, fine-grained soils.

Biological soil crust stands were found more frequently in areas with sparse vascular vegetation cover than in areas with dense cover or in areas with no vascular plants (Table 4). Lower levels of biological soil crust development (LOD 1–3) were observed on dunes that appeared active in the 2009 aerial photographs but that had started to stabilize by 2011 (Table 4). Soil crusts were rarely observed in areas where dunes appear stabilized in the 1929 aerial photographs, where the vascular vegetation ground cover is dense and composed predominantly of the annual grassland community. Areas that stabilized between 1929 and 2009 contain more soil crust stands and exhibit a wide range of crust LODs (Table 4).

Soil Particle Size Analysis

The particle-size distribution of the 30 soil samples collected within the study area shows a trend towards an increase in fine silt and clay content of soils with higher biological soil crust LOD. The control samples, which displayed no visible biological soil crust development, contained an average of 1.9% fine silt and clay. Samples with low levels of biological soil crust development (LOD 1–3) contain an average of 2.2% fine silt and clay. In contrast, samples with higher levels of biological soil crust development (LOD 4–6) contain an average of 17.6% fine silt and clay. The sand content is high, as expected, in all of the samples, ranging from 60.3% to 99.4%. The coarse silt content of the samples is consistently very low, ranging from 0% to 3.4%, with a slight increase in higher levels of biological soil crust development (LOD 4–6).

Three samples classified as high LOD do not show a significant increase in fine silt and clay. During the dispersant removal process, these samples had very fine particles that remained in suspension despite repeated centrifuging. Thus, many of these fine particles were likely removed when the supernatant was poured off the samples during the washing process. Therefore, these outliers may not accurately represent the fine silt and clay content of the original samples.

DISCUSSION

Patterns of Change in Vegetation Communities on Stabilizing Dunes

The results of both aerial photo analysis and field surveys demonstrate that total vegetation cover on San Miguel Island has been steadily increasing since the removal of grazing animals, despite multiple periods of low-rainfall or drought conditions (Fig. 2). The active dune extent in the Central Dune Field has dwindled from 12.8 km^2 in 1929 to 0.9 km^2 in 2009, with an average decrease of about 50% every 25–30 years. On the dunes that stabilized most recently (between 2009 and 2011), 75% of the area surveyed was covered with vegetation with an average canopy cover of 25%; only 25% of survey points fell on exposed sand or soils. On dunes that stabilized before 1929 and between 1929 and 2009, 100% of survey points were within vegetated areas, and the average canopy cover of all the plant communities in those areas ranged from 80% to 93%, with similar or decreasing amounts of variation in cover over time (standard deviations in the range of 26%–13%).

In some postgrazing decades, rainfall was as low as it was during some droughts that contributed to the reactivation of dunes during the periods of heaviest grazing (e.g., Johnson 1980; Fig. 2). Perhaps in the case of San Miguel Island, short-term rainfall variability does not pose a major threat to the dune vegetation in the absence of other disturbances. This hypothesis contrasts with studies conducted in the Great Plains of North America. For example, Muhs and Holliday (1995) found that droughts, which result in diminished vegetation cover, were likely a contributing factor to the dune reactivation that occurred during the 19th century in Nebraska, Colorado, Kansas, New Mexico, and Texas. Both San Miguel Island and the Great Plains of North America have semiarid environments. However, San Miguel Island is frequently engulfed in a dense fog due to the atmospheric marine layer that surrounds the island. Without additional disturbance, such as grazing, this fog may contribute enough additional moisture to sustain dune vegetation during dry periods.

High grassland cover was found on dunes that appeared stabilized in the 1929 aerial photographs. High pioneer coastal dune scrub cover was found on dunes stabilized since 2009, but overlaps in vegetation community types were present on dunes that appear stabilized in the 3 sets of photographs that represent intermediate periods (1929–1954, 1954–1977, and 1977–2009; Fig. 6). These overlaps indicate that there may be more than one successional pathway present on the stabilized dunes within the study area, or that succession does not follow a linear trajectory. In recently stabilized areas (i.e., areas stabilized between 2009 and 2011), the pioneer coastal dune scrub community is clearly the first vegetation community to colonize the active dunes. The mixed coastal dune scrub community was also found in these recently stabilized areas and appeared to be associated with the pioneer coastal dune scrub community based on field observations; however, the methods used in this study did not allow quantification of how long it takes for the pioneer coastal dune scrub community to transition into this more diverse community. Because the mixed coastal dune scrub community was rarely encountered on any dunes, it may have a short-lived, transitory, or variable role in succession. This community may only develop in certain topographic settings. In addition to the 2 coastal dune scrub communities, dunes at the earliest stages of stabilization included a small proportion of the exotic iceplant community.

During the intermediate periods examined (1929–1954, 1954–1977, and 1977–2009), dunes were mostly covered with native woody shrub communities—mixed goldenbush scrub, lupine scrub, coyote-brush scrub, and coreopsis scrub—in fairly similar proportions in each of the 3 time periods (Fig. 6). According to Sawyer and Keeler-Wolf (2009), studies from coastal dunes on the California mainland have shown that the lupine scrub community invades areas that were previously stabilized by coastal dune scrub. Later, the coyote-brush scrub community invades the areas that were previously colonized by lupine scrub. Because the transitions among these communities occur relatively rapidly, it was not possible to determine if the same pattern is represented on the San Miguel Island dunes, or if succession is occurring along multiple or cyclic pathways. Perhaps, in the selection of 25-year

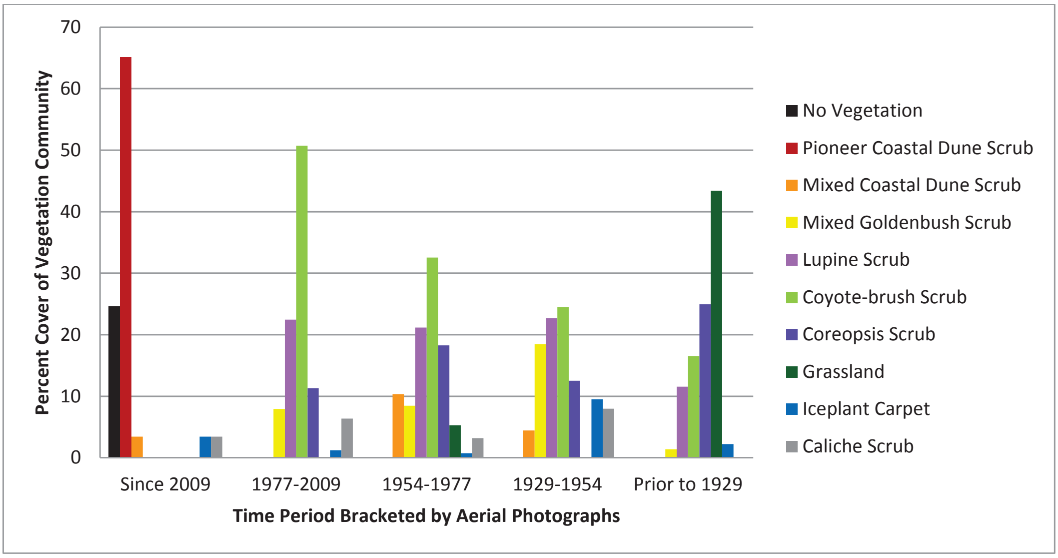

Fig. 6. Vegetation communities by time period. There are distinct differences in the vegetation communities present on dunes at both the oldest (prior to 1929) and the most recent (since 2009) periods but overlaps in vegetation community patterns for the 3 intermediate periods (1977–2009, 1954–1977, and 1929–1954).

intervals for analysis, dunes with more and less recent disturbance histories within those time frames were pooled together. This situation might have minimized the differences that existed among intermediate phases of succession. Alternatively, the presence of all 4 of the native shrub communities across the chronosequence could be the result of variations in environmental conditions across the study area, such as topography and soil moisture (Corry 2006).

Within the study area, the combined coverage of the native mixed goldenbush scrub, lupine scrub, coyote-brush scrub, and coreopsis scrub communities decreased with longer periods of stabilization, whereas the coverage of the exotic grassland and iceplant carpet communities increased. Some of the increased occurrence of grassland in areas that were stable in the 1929 aerial photographs may be attributed to soil texture, considering that over half of the area surveyed (55%) contained dark, fine-grained soils. Many studies have found an association of exotic grasslands with finer-grained soils (e.g., Hobbs 1983, Young et al. 1999), presumably because the lower permeability favors the shallow-rooted grasses and allows less moisture to percolate to the rooting depth of perennial plants (Corry 2006). However, this does not explain the increase in grassland on the stabilized dunes that are composed of sandy soils. It is possible that the exotic grasses colonize sandy soils only after they have been altered by many years of native vegetation succession. The grasses may then outcompete the native vegetation for soil moisture, thus eventually replacing the native-dominant communities with exotic-dominant grassland community. A second, and perhaps more likely, possibility is that the stabilized dunes in the 1929 aerial photographs were colonized initially by invasive grasses, and these exotic communities have persisted over time. Exotic grasses are often more tolerant to anthropogenic impacts than native vegetation (D'Antonio and Vitousek 1992). In the case of San Miguel Island, the majority of the grazing livestock was removed prior to 1929. However, some grazing animals were present until 1966. During the early periods of stabilization, when the landscape was still experiencing some degree of grazing pressure, exotic grasses may have been the species most capable of growing on the dunes.

The caliche scrub community occupies all areas where a petrocalcic horizon is exposed, indicating that the community is edaphically specialized to these unusual conditions. Also, the caliche scrub community shows little to no change in distribution over time. It is possible that, prior to grazing, soils had not eroded to an extent that resulted in exposure of the petrocalcic horizon at the surface. Thus, the caliche scrub community may not have existed prior to grazing. The lack of caliche scrub communities and exposed petrocalcic horizons in areas that were stabilized in the 1929 aerial photographs could indicate that these areas were not affected as severely, or at all, by the most recent vegetation denudation episode. Large sections of this area consist of dark, fine-grained soils that were developed in parent materials other than dune sand. These soils may have been affected differently by grazing than the areas of stabilized dunes. However, nearly half (45%) of the study area that appears stable in the 1929 aerial photographs consists of stabilized dune sand. Since the caliche scrub community is not found in areas stabilized in the 1929 aerial photographs, the 1929 aerial photographs may display nearly the full spatial extent of the denudation of vegetation that resulted from overgrazing.

The Role of Biological Soil Crusts in Dune Stabilization

The amount and LOD of the biological soil crusts vary across the time periods represented by the aerial photographs. Low biological soil crust LODs are associated with the dunes that have been stabilized the longest (in the 1929 aerial photographs) and with the dunes that have recently been stabilized (2009–2011). In contrast, higher biological soil crust LODs are associated with dunes that stabilized during the intermediate time periods (1929–1954, 1954–1977, and 1977–2009). Furthermore, the amount of biological soil crust stands generally increases with decreasing percent cover of vegetation. However, it is apparent that at least sparse vegetation cover is a prerequisite to biological soil crust development on the San Miguel Island dunes. Stands of crust were found near the base of vascular plants nearly everywhere they occurred, and they were typically small (<50 cm in diameter), indicating that fog drip from vascular plants may play a critical role in biological soil crust development on San Miguel Island. However, although biological soil crusts were never found in the absence of vascular plants, many areas had vascular plants but lacked crusts. These findings contrast with several studies, mostly from Israel, that found biological soil crust covering vast expanses of many dunes and acting as a *primary* stabilizer (Danin and Yaalon 1982, Tsoar and Moller 1986, Danin et al. 1989, Hesp 1991, Leys and Eldridge 1998, Levin et al. 2007).

The contrast between the extensive biological soil crust development on Israeli dunes and their limited development on San Miguel Island dunes may be explained by differences in the amount of dust available for capture by established biological soil crust stands. It is well accepted that biological soil crusts reach higher LODs through the trapping of atmospheric dust (Belnap 1994, 2001, Williams et al. 2013). Indeed, the particle-size analysis on samples collected from the study area revealed that there is a trend toward more fine silt and clay particles in soils with higher LOD classifications. Heavy dust storms are common in Israel, with an average of 19 storms occurring each year (Ganor 1994). These wind events transport suspended particles of fine silt and clay from the Sahara Desert over the Mediterranean Sea. Much of the dust, however, settles en route over Israel (Ganor 1991, 1994). Similarly, Santa Ana wind events transport fine silt and clay particles from drainages in the coastal mountains of southern California and the Mojave Desert to the eastern Pacific Ocean and the California Channel Islands (Muhs et al. 2007). However, satellite imagery taken during a Santa Ana event on 6 January 2002 shows that San Miguel Island is located outside the path taken by typical Santa Ana wind events. It is also likely that the amount of sand saltation is higher on San Miguel Island, which could explain why stands of cyanobacteria are common on the dunes, but mosses and lichens are rarely encountered. Cyanobacteria thrive on active dunes because they are motile and capable of moving to reclaim soil surfaces after burial by a thin layer of sand (Williams et al. 2013). As Belnap (1994) explains, this adaptation allows cyanobacteria to bind soil particles far below the depth to which light can penetrate, thus facilitating some degree of increased soil stability while still allowing for moderate saltation. In contrast, mosses and lichens require a stable substrate, and are unable to grow on soils experiencing even moderate sand saltation (Williams et al. 2013).

The occurrence of biological soil crusts in early and intermediate phases of dune stabilization, as well as the absence of crusts on active dunes and those that stabilized prior to 1929, may indicate that the role of crusts in the stabilization process is transitory. Although biological soil crusts were not widespread on the San Miguel Island dunes, their importance should not be underestimated. Their presence on the dunes likely facilitates vascular vegetation development and patterns of change in vegetation communities. The extensive amount of laboratory time required to remove the organic matter from soil samples that contain biological soil crusts is a testament to the ability of these organisms to bind soil particles together. During drought years, when vascular vegetation is stressed, the binding properties of the biological soil crusts that develop at the base of plants may be the only protection from soil loss due to erosive forces (Eldridge and Leys 2003).

Implications for Management and Future Research Directions

The results of this study have important implications for the management of coastal sand dunes within the Channel Islands National Park. The finding that vascular vegetation, not biological soil crust, is the primary stabilizer of the San Miguel Island dunes indicates that the stabilization of the dunes could be threatened by periods of prolonged aridity. Nevertheless, the vegetation communities appear to be resistant to short-term dry periods, because the aerial photograph record reveals a continual increase in total vegetation cover despite the multiple low-rainfall years that have occurred since the removal of grazing sheep. The findings presented here indicate that vegetation cover will likely be sustained, or continue to increase, in the absence of major changes in climate conditions and other disturbances. The National Park Service has already limited disturbances to the San Miguel Island dunes through the removal of nonnative animals and a strictly controlled visitor program, allowing the dunes to continue to stabilize over time. However, the observation that the longest-established vegetation communities in the study area were dominated by exotic grasses, and that some exotic species were present on dunes at each of the 5 time periods examined, suggests that native vegetation communities on the dunes may be vulnerable to encroachment by exotic plants during the later stages of succession.

This study represents a pilot assessment of many aspects of dune vegetation community development on San Miguel Island since 1929. Future studies could utilize a more systematic sampling design and regular (ideally annual) monitoring of vegetation and biological soil crusts to identify relationships among physical and ecological processes and factors. It may be especially important to focus on dunes at the earliest and latest stages of stabilization, in which—based on results presented here—the most rapid and/or significant changes to vegetation communities may occur. The rapid nature of vegetation community establishment is evident from the finding that some of the dunes shown as active (100% exposed sand) in the aerial photo from 2009 had 75% vegetation cover and 25% exposed sand only 2 years later, in 2011. The average canopy cover of the communities in these areas was considerably lower (25%, SD 32%) than on dunes that had stabilized at earlier times; average canopy covers of 81%–87% (SD 26%–20%), respectively, were measured for vegetation communities on dunes that stabilized between 2009 and 1929. The striking differences in vegetation community types and cover in the earliest period (in the 1929 aerial photographs) compared to the subsequent period (1929–1954) suggest that monitoring newly stabilizing areas over 1–25 years would clarify when and how shifts in communities take place, as well as reveal the possible role of biological crust formation in these processes. An abrupt transition is also evident in the finding that a high percentage of nonnative grassland communities was present on dunes in the 1929 aerial photographs (43% cover of exotic grasses) in contrast to dunes in all periods occurring after 1929 (0%–10% grassland community).

Monitoring "older" dunes might reveal the times and conditions at which encroachment of native shrub communities by exotic species is most likely to occur and the factors influencing the disappearance of biological soil crusts in these areas. To evaluate relationships among ecological and physical processes more thoroughly, permanent monitoring plots or transects could be established in locations identified from the GIS layers in the present study that represent the diversity of topographic positions, slopes, aspects, and insolation across the study area, in addition to capturing a gradient of time since stabilization. Within plots or transects, it should be possible to measure percent cover and diversity of vegetation and biological soil crusts using the same methods in order to facilitate comparisons and analyses that were beyond the scope of the present study. Ideally, there could be equal sampling in all the conditions of interest; the distribution of the transects in the present study across the Central Dune Field resulted in an unbalanced sample size among the time periods that were compared, and many transects included sections from multiple periods. Although an attempt was made to account for this by applying a spatial buffer to the selection of sample points, the methods could be improved in future studies to allow a more clear test of possible differences among communities of vegetation and biological soil crust over time and a more thorough statistical analyses of the relationships identified. If annual field-based vegetation monitoring is not feasible, recent high-resolution multispectral satellite imagery and remote sensing software could be used to identify vegetation communities by spectral signatures, thus enabling a tracking of successional changes over time. If a remote sensing approach is utilized, vegetation communities identified by spectral signature could be verified with ground-truth data collected during the same year and season as the satellite imagery.

A future study could investigate if other environmental conditions are limiting factors for specific vegetation communities and biological soil crust development. Factors such as slope angle, aspect, and wind exposure can all be quantified through remote sensing. The 2010 LiDAR digital elevation model for San Miguel Island could be used to derive products such as hillshades, slope maps, and aspect maps. These maps could then be combined with data on the spatial distribution of vegetation communities and biological soil crust stands in a GIS. Spatial analysis could then be performed to identify patterns in vegetation communities that relate to these topographic conditions.

CONCLUSIONS

A steady increase in vegetation cover and a complex pattern of change in vegetation communities on the San Miguel Island dunes followed disturbance by grazing animals in the late 19th and early 20th century.

The highly specialized vascular plants in the pioneer coastal dune scrub community are the first to colonize recently active dunes. These colonizers are followed by the transitory mixed coastal dune scrub community. At later stages, multiple native shrub-dominated communities develop as the pioneer coastal dune scrub and mixed coastal dune scrub communities decline in cover, indicating that the trajectory of vegetation succession is not linear. Long-term vegetation monitoring, beyond the scope of the present study, may identify the mechanisms or abiotic factors that may influence successional change in plant communities on San Miguel Island.

Dunes that appear stabilized in the 1929 aerial photographs are dominated by exotic vegetation communities, and exotic plants are present in the understory on dunes that stabilized between 1929 and 2011. This result could indicate that exotic species outcompete the native vegetation communities in later stages of dune stabilization. Alternatively, exotic species may have been the only plants capable of growing on the dunes during the early periods of stabilization while some nonnative herbivores were still on the island, and these exotics have persisted for nearly 100 years.

A continuing increase in total vegetation cover occurred as grazing decreased and then ceased, despite multiple dry periods. This indicates that the vascular vegetation communities are resistant to relatively low rainfall and drought conditions, at least over short periods, in the absence of other disturbances.

The occurrence of biological soil crusts in early and intermediate phases of dune stabilization and disappearance of biological soil crusts with increasing vegetation cover may indicate that their role in dune stabilization on San Miguel Island is transitory. The abundance of cyanobacteria and rare occurrence of mosses and lichens are likely due to the amount of sand saltation present on dunes in early stages of stabilization, combined with a lack of fine-grained particles. The transitory nature of biological soil crusts on San Miguel Island contrasts with crust development on desert dunes in Israel, where abundant fine-grained particles are deposited on the dunes from the Sahara Desert during dust storms and biological soil crusts are a primary stabilizer of dunes.

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