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COMPARISON OF DISTURBANCE IMPACTS TO AND SPATIAL DISTRIBUTION OF BIOLOGICAL SOIL CRUSTS IN THE LITTLE SAN BERNARDINO MOUNTAINS OF JOSHUA TREE NATIONAL PARK, CALIFORNIA

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ABSTRACT.—Biological soil crust ecology in the hot Mojave Desert is poorly understood with regard to crust distribution and abundance, as well as the impacts of trampling disturbance on crust development. Our objective was to study biological soil crusts in 2 areas of differing disturbance pressures in the high desert region of Joshua Tree National Park, California, with respect to visible crust cover and frequency, chlorophyll *a*, and soil stability. Impacts on biological soil crusts from 2 disturbance regimes, historic grazing and recent high foot traffic, were compared using a disturbance indicator. In addition, we measured a suite of abiotic and biotic soil parameters commonly associated with crust abundance and distribution and characterized occurrence with respect to 3 geomorphic features (pockets, slopes, and wash banks).

Individual physical and chemical soil parameters historically have been associated with crust development. In contrast, this study demonstrates that geomorphic features with a suite of soil properties clearly impacted crust development. In both study areas, wash banks showed the best crust development (51%–52% total crust cover) and slopes showed the poorest crust development (<37% total crust cover). Lichens and mosses were best developed in the pocket areas (1.1% and 1.5% cover, 25%–30% frequency), which can accumulate and retain moisture during and following precipitation events.

Our disturbance index suggested that the high-foot-traffic area, being associated with a reduction in visible crust cover, has experienced more recent disturbance than the historically grazed sites. However, despite the reduction in cover, the high-foot-traffic area had more lichen and moss crusts, indicating that the crusts in this area are more successionally mature. In contrast, the historically grazed area showed clear signs of recovery from past grazing disturbance, with a higher visual cover of biological soil crusts. However, crusts also had lower biomass values, supporting an earlier successional stage. Overall, we conclude that biological soil crusts of the Mojave Desert are very different in composition, form, and ecology than crusts of other desert regions of North America.

RESUMEN.—La ecología de la corteza biológica del suelo en el caluroso desierto Mojave es poco entendida con respecto a su distribución y abundancia, así como el impacto de las perturbaciones en el desarrollo de la corteza causadas por el pisoteo. Nuestro objetivo fue estudiar las cortezas biológicas de 2 áreas con diferentes presiones de perturbación en la región alta del desierto del Parque Nacional Joshua Tree, California, con respecto a la cobertura visible y la frecuencia de la corteza biológica, laclorofila *a* y la estabilidad del suelo. Los impactos en la corteza biológica de 2 regímenes de perturbación, el pastoreo histórico y la frecuencia de pisoteo reciente fueron comparados utilizando un indicador de perturbación. Además, medimos un conjunto de parámetros abióticos y bióticos del suelo comúnmente asociados con la abundancia y distribución de la corteza y caracterizamos su incidencia con respecto a 3 características geomorfológicas (hondonadas, pendientes y bancos de deslave).

Los parámetros físicos y químicos individuales del suelo han sido asociados historicamente con el desarrollo de la corteza biológica. En contraste, este estudio demuestra que las características geomórficas, aunadas a un conjunto de propiedades del suelo, claramente impactaron el desarrollo de la corteza. En ambas áreas de estudio, los bancos de deslave mostraron el mejor desarrollo de la corteza (51%–52% de la cobertura total de la corteza) y las pendientes exhibieron el peor desarrollo de la corteza (<37% de la cobertura total de la corteza). Los líquenes y musgos se desarrollaron mejor en las hondonadas (1.1% y 1.5% cobertura, 25%–30% frecuencia), las cuales pueden acumular y retener humedad durante y después de las precipitaciones.

Nuestro índice de perturbación, el cual estuvo asociado con una reducción en la cobertura visible de la corteza biológica, sugirió que el área con alto pisoteo ha experimentado perturbación más reciente que los sitios históricamente pastoreados. Sin embargo, a pesar de la reducción en la corteza, el área con alto pisoteo tenía más cortezas de líquenes y musgos, lo cual indica que las cortezas en esta área son sucesionalmente más madura. En contraste, el área históricamente pastoreada mostró claros signos de recuperación de una perturbación anterior por el pastoreo, con una mayor cobertura visual de la corteza biológica del suelo. Pero también tuvieron valores menores de biomasa, indicando un estado sucesional más temprano. En general, concluimos que las cortezas biológicas del suelo del desierto Mojave son muy diferentes en composición, forma y ecología que las cortezas de otras regiones desérticas de Norteamérica.

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In western North America, biological soil crusts can be found in various ecoregions and ecosystems: the coastal woodlands of northern California, Oregon, and Washington; the chaparral and coastal sage scrub of southern California; the subhumid grasslands of the Great Plains; and in all 4 deserts of the southwestern United States (Rosentreter and Belnap 2003). Biological soil crusts are surface soil features in which cyanobacteria, green algae, fungi, lichens, and mosses consolidate the soil (Evans and Johansen 1999). Other microbes, such as bacteria and protists, are associated with these crusts but likely do not assist in aggregation. Biological soil crusts are ubiquitous in soils where there is no strong competition for resources with vascular plants (Eldridge et al. 2000). These crusts have been implicated in several desert ecosystem processes, such as nitrogen fixation, organic matter accumulation, soil stability, and water relations (Johansen 1993).

Numerous reviews (West 1990, St. Clair and Johansen 1993, Evans and Johansen 1999) and hundreds of studies have been conducted concerning the morphology, taxonomy, and ecology of biological soil crusts around the world in all vegetation zones (see Belnap and Lange 2003). However, most research in the desert environments of western North America has been concentrated on the cold desert or semiarid steppe habitats. There is far less information concerning crust development and ecosystem function in the hot deserts of North America (i.e., Sonoran, Chihuahuan, and Mojave Deserts).

Johansen et al. (2001) demonstrated that physical disturbance from off-road vehicles was the primary factor limiting crust distribution and abundance of soil crust at 27 study sites in the western Mojave Desert of California. In addition, they concluded that biological soil crusts are thinner, more fragile, and less visible in creosote scrub habitats, and, for reasons not apparent in that study, can be completely lacking in seemingly pristine undisturbed areas. Additionally, lichens and mosses show a more limited distribution and lower diversity in the Mojave Desert compared to the Great Basin Desert (St. Clair et al. 1993, Johansen et al. 2001, Pietrasiak et al. 2011).

Due to a more patchy distribution, biological soil crusts apparently play a more minor role in soil stabilization in the Mojave Desert than in cool deserts, such as the Colorado Plateau (Belnap et al. 2007). Biological soil crusts in the Mojave Desert share this role in soil stabilization with other landsurface features, such as chemical crusts, grusy soils, and rocky surface cover. However, if biological soil crust disturbance occurs, stabilized thin topsoil will be lost and recovery will take many years (Stark et al. 1998).

Comparisons between different disturbance regimes are rare, and though grazing and fire have been compared (Johansen et al. 1982, 1993, 2001, Brotherson et al. 1983, Johansen and St. Clair 1986, Eldridge et al. 2000), different types of trampling disturbance rarely have been compared (Belnap et al. 2007). The impacts of trampling, particularly foot traffic, on soil crusts and vegetation is of great interest to land managers at Joshua Tree National Park, especially in light of the popularity of rock climbing as a recreational sport in the park. Over 30% of park visitors rock climb, and one of the major impacts of this activity is the proliferation of social trails accessing the climbing sites (Camp 1995, Le et al. 2004, Murdock 2004, Kaempfen 2006). The most impacted area in the park, commonly referred to as the Wonderland of Rocks, is the focus of this study.

The objectives of our study were threefold: (1) to determine the spatial distribution of biological soil crusts in a high desert region of the southwestern Mojave Desert; (2) to compare 2 areas of differing disturbance regime within that region: historic grazing impact (in recovery) versus current human foot traffic (in degradation); and (3) to detect factors determining crust development in the Mojave Desert, including soil and geomorphic characteristics.

METHODS

Study Area

Both study areas are in the Little San Bernardino Mountains of southern California, San Bernardino County (ca. 34°N, 116°W), embedded within the Mojave Desert region of Joshua Tree National Park. The study areas are referred to as Keys Ranch Area (KRA) and North Barker Dam (NBD) in reference to their location within the park. These sites are both found within the highly visited region of the park known as the Wonderland of Rocks, which is in the northwestern portion of the park. The Wonderland of Rocks area is part of a major granite pluton intrusion. The dominant rock is the Cretaceous White Tank Monzogranite or Monzanite

(Trent 1984). This granite is easily weathered and breaks up to form a loose grus (unconsolidated coarse sand and fine gravel surface layer) found in the regolith. The soils are mainly shallow Entisols.

The climate in Joshua Tree National Park is that of an arid, midlatitude, rain shadow desert. The precipitation of this hot desert falls in 2 periods during the year; during winter, it falls as mild rains or occasionally snow, and during summer, the monsoon thunderstorms can deliver large but isolated rain events causing flash floods (Trent 1984, Trent and Hazlett 2002). Rain events demonstrate variability in temporal and spatial distribution that is typical of arid regions (Osborn 1983). Near the study site, average annual temperature is 16 °C with annual precipitation of 160 mm, based on data collected over the last 10 years at the nearby Lost Horse weather station (http://cdec.water.ca.gov/cgi-progs/staMeta?station_id=LTH).

Both areas belong to the Mojave Yucca Woodland Community dominated by Scrub Oak, Mojave Yucca and Pinyon Pine (modified after Munz 1974). Common trees and shrubs included *Quercus cornelius-mulleri, Pinus monophylla, Yucca schidigera, Nolina parryi, Ericameria cuneata,* and *Eriogonum fasciculatum.* Dominant perennials were *Lotus rigidus, Dudleya saxosa, Gutierrezia microcephala, Opuntia basilaris, Opuntia phaeacantha, Pleuraphis rigida,* and *Achnatherum speciosum.* Major annuals consisted of *Phacelia* spp., *Cryptantha* spp., *Eriophyllum wallacei, Salvia columbariae, Chamaesyce albomarginata, Pectocarya setosa,* and *Chaenactis* spp. Introduced exotics, such as *Sisymbrium altissimum, Schismus barbatus, Bromus madritensis* ssp. *rubens, Bromus tectorum,* and *Erodium cicutarium,* were present in both areas.

The 2 study areas were similar in all ways (e.g., geomorphology, vegetation) except for their disturbance history; both areas were designated Federal Wilderness in 1994. The first area, NBD (Fig. 1A), was inaccessible to cattle and has had a long, relatively disturbance-free, period of time in which crusts could develop. However, NBD has experienced increased trampling disturbance recently from hikers and rock climbers over the last 20 years. The second area, KRA (Fig. 1B), was part of a ranching operation and was heavily grazed by cattle for over 60 years (ca. 1870–1964). KRA was also disturbed by human activities until 1994, when it was closed to all visitation.

Study Plot Characterization

Initial field visits identified suitable study plots within the 2 study areas (KRA and NBD), defined as areas with at least 5 m^2 and a maximum 100 m^2 of exposed soil with no large breaks (e.g., large boulders, rock outcrops, large trees, or woody perennials). At each plot, the following parameters were recorded: GPS coordinates (UTM, NAD83 datum), elevation, size of plot, a disturbance indicator, and a geomorphic classification.

The size of the plot was estimated by measuring the longest axis of the study plot area and the width of its perpendicular axis. The disturbance indicator consisted of 4 categories: (1) no disturbance—lacking obvious disturbance, footprints, or trampling; (2) minor disturbance—few footprints but no trail; (3) medium disturbance—light trail but not heavily compacted and/or evidence of footprints on the site; and (4) heavy disturbance—obvious hardened trails and/or footprints covering more than 50% of the site.

Additionally, each plot was categorized based on geomorphic features into one of the following 3 categories: pockets, slopes and wash banks (Fig. 2). Wash banks were found along the ephemeral stream channels, were often linear in shape, and were subject to frequent flooding events. The slope of a wash bank was generally greater than 10° and the surface contained less gravel (Fig. 2A, Table 1). Slopes were defined as erosional surfaces with steep slopes (5°–10°). They were generally located just above the stream channels and had the greatest surface area (Fig. 2B, Table 1). Pockets were defined as shallow depressions enclosed by bedrock or large boulders, with no slope or gentle slope (<5°) (Table 1). Twidale (1982) described such pockets as "pans," a type of rock basin where grus remains in the depression. Pockets contained an accumulation of soil material, were usually elliptical in shape, and were not subject to flooding because of their location above the stream channels in bedrock (Fig. 2C). Mean slope of the 3 geomorphic features was very similar in the 2 areas (Table 1), and the grand mean for slope and the relative position of the features are illustrated in Fig. 2D. All possible aspect directions were detected (Pietrasiak 2005).

A total of 274 study plots were located in the 2 study sites. Out of this pool of sites, 20 pockets, 20 slopes, and 10 wash bank plots were randomly selected from each area for a total of 50

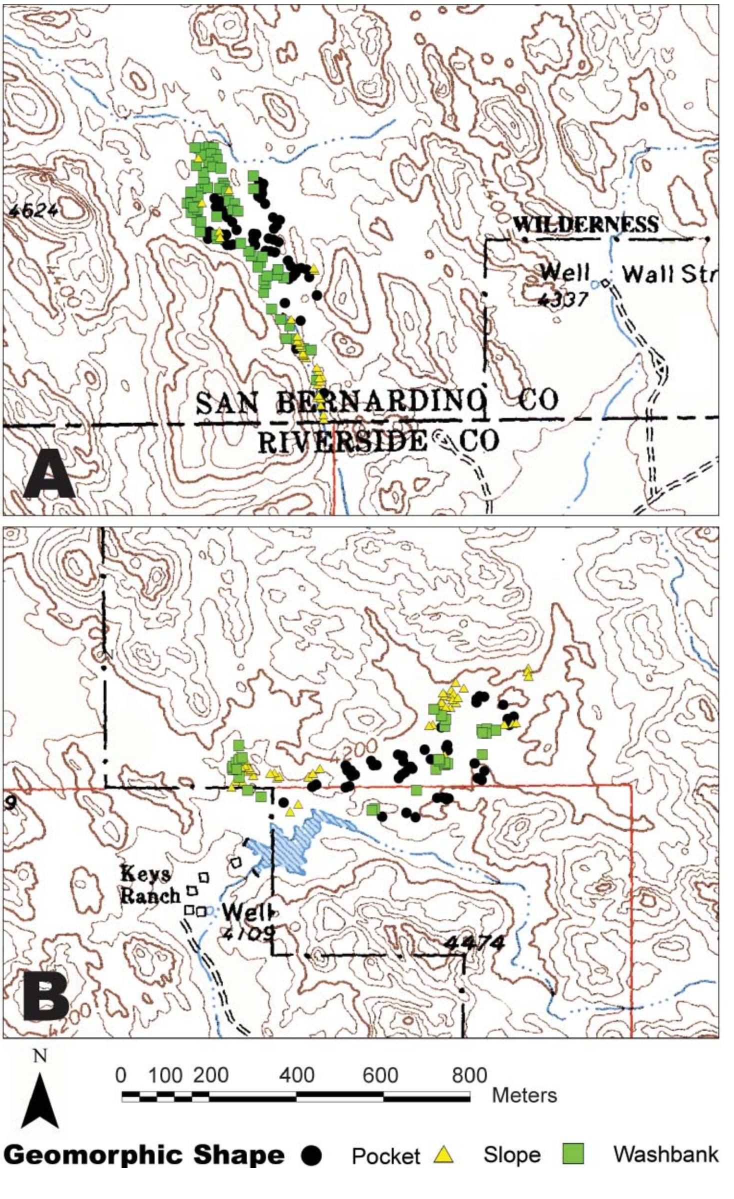

Fig. 1. Maps of the study areas in the Little San Bernardino Mountains of Joshua Tree National Park, California: A, North Barker Dam; and B, Keys Ranch Area.

plots per study area. Only 10 wash bank plots per area were selected due to the low occurence of this geomorphic feature. Each plot was visited between April and June 2004. A quadrat sampling protocol was used to (1) record cover and frequency of vascular plants, soil crust, and nonliving material; (2) measure soil stability; and (3) collect soil cores. The vegetation at each plot was recorded and is available in Pietrasiak (2005).

Biological Soil Crust Characterization

In order to accommodate the varying plot sizes of the soil islands, the sampling protocol consisted of laying a tape measure along the longest axis of the plot. Quadrats (0.25 m^2) were placed along this axis every 3 m, starting at 1 m, until the edge of the plot was reached. In addition, perpendicular axes were used starting at meter 4; these quadrats were placed

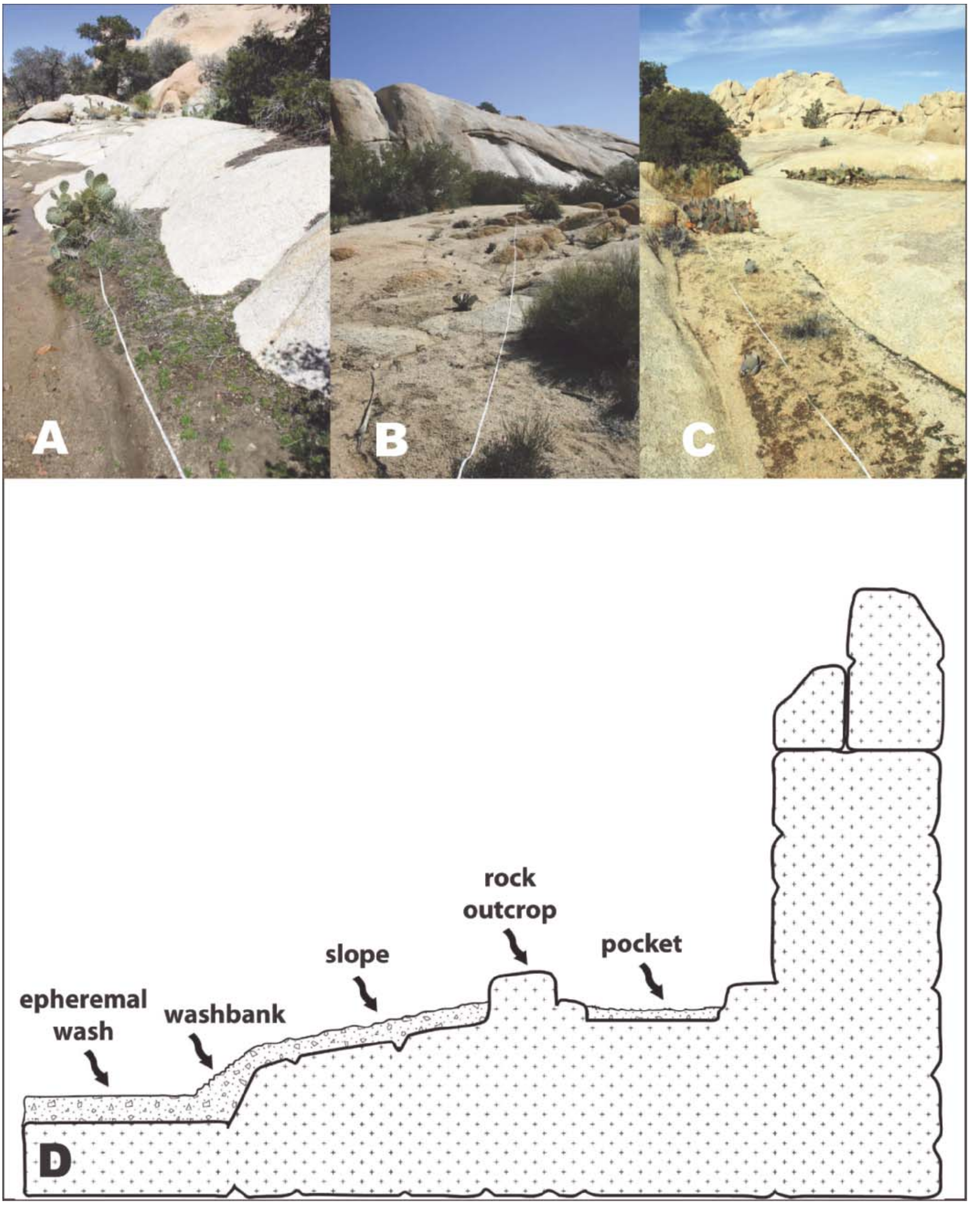

Fig 2. Photographs and scheme of geomorphic features: A, steep-sided wash bank rising from the ephemeral stream bed; B, slope area positioned between the upslope pocket areas and downslope wash bank; C, typical pocket area showing rugose crust development; and D, scheme of the geomorphic features in this study.

at increasing intervals and on alternating sides of the long axis. For example, at quadrat 2 (4 m), the perpendicular quadrats were placed to the right every 1 m until the series of quadrats hit the edge of the plot, whereas at quadrat 3 (7 m), the perpendicular quadrats were placed every 2 m to the left, and so on. For plots less than 11 m in length, the intervals were adjusted in order to achieve a minimum of 5 quadrats per plot.

A point-cover method (Bonham 1989, Marble and Harper 1989) was used to estimate ground cover for the following categories: (1) vascular

TABLE 1. Means for selected measured field data in 2 areas of Joshua Tree National Park. Means are summarized by geomorphology. Significance probability values are reported for main effects only (study area: NBD, KRA; geomorphology: pocket, slope, wash bank). The geomorphic feature with the highest mean is indicated in lowercase letters following the probability value (p = pocket, s = slope, w = wash bank).

	North Barker Dam (NBD)			Keys Ranch Area (KRA)				
Field parameter	pocket	slope	wash bank	pocket	slope	wash bank	Area *P*	Geomorph. *P*
Slope (°)	3.7	10.0	12.5	3.2	8.4	14.9	0.925	<0.001 w
Area (m^2)	33.8	87.7	10.9	44.6	55.0	9.3	0.498	<0.001 s
Stability index	3.6	2.8	5.6	4.6	3.8	4.7	0.062	<0.001 w

plants—annual vegetation, perennial grasses, and woody and nonwoody perennials; (2) biological soil crust types—visible algal crust, lichen crust, moss crust, and mixed crust (algal crust with thalli of lichen and mosses smaller than 1 cm^2; Eldridge and Rosentreter 1999, Belnap et al. 2001); and (3) nonliving material—plant litter, bare soil without crust, gravel, rock, and anthropogenic litter. Twenty-five points were taken in each 0.25-m^2 quadrat using a grid of strings.

A nested frequency quadrat method (Bonham 1989, Marble and Harper 1989) was applied to record the occurence of objects in quadrats of specified sizes. A frequency value was assigned to the same categories as the ground cover analysis, using a nested frequency protocol to determine which size quadrat was appropriate for each category. The sizes of the 6 nested quadrats were 0.25 m^2, 0.125 m^2, 0.0625 m^2, 0.03125 m^2, 0.015625 m^2, and 0.0025 m^2.

Surface (0–0.5 cm) and deep (0–3.0 cm) composite samples were taken at each plot for chlorophyll *a* analysis. Three 1.5-g subsamples from each composite sample were analyzed, except for some surface samples for which sufficient material for only 2 replicates was available. Samples were extracted in the dark with 5 mL DMSO (dimethylsulfoxide) for 60 minutes and afterwards were shaken and centrifuged for 10 minutes at 1700 RPM. The suspension was then filtered through glass fiber filters. Chlorophyll *a* was measured using a Turner Model 450 Fluorometer (Johansen et al. 2001). Chlorophyll *a* values are reported in μg chlorophyll *a* per g soil.

Soil Characterization

Surface soil stability was tested in each cover quadrat using the soil stability test described in Herrick et al. (2001). Soil samples were taken at the top left corner of each quadrat for 2 depths and composited. Each plot then had 2 composite soil samples: one representing a narrow depth interval of 0–0.5 cm and one representing a broader sampling interval of 0–3.0 cm. These samples were used in the chemical and physical laboratory tests described below.

Soil samples from both depths were air-dried for 24 hours then sieved through a 2-mm sieve. Soil crust was crushed through the sieve to combine with the fine earth fraction. Percent gravel was determined gravimetrically. All other analyses were carried out on the fine earth (<2 mm) fraction. Air-dried fine earth samples (90 g) were used for the particle size analysis. If not enough soil material was available, 70-g or 50-g samples were used instead. The determination was done using a modified Bouyoucos hydrometer method (Bouyoucos 1951, Gee and Bauder 1986).

Soil samples were ground and passed through a 150-μm sieve. This powdered material was sent to the USDA Forest Service Lab, Flagstaff, Arizona. Total carbon (TC) and total nitrogen (TN) were determined by dry combustion with an elemental analyzer Model no. NA 1500 Series 2, Carlo-Erba Instruments, Milan, Italy (Nelson and Sommers 1996).

Saturated paste was prepared for all samples (United States Salinity Laboratory 1954). After 10 minutes, pH values were detected using a glass electrode pH meter (Fisher Scientific, Accument® Model 25). Following pH determination the saturated pastes were mixed again and left overnight. The following day, soil extract was collected using a vacuum apparatus. Electrical conductivity was determined from the soil extract with a field EC meter (Model Horiba Compact Conductivity Meter C172/173).

Data Analysis

Comparisons among the 2 areas and 3 geomorphic forms were made using multifactor ANOVA in the statistical software package SPSS. In addition, linear regression and correlation

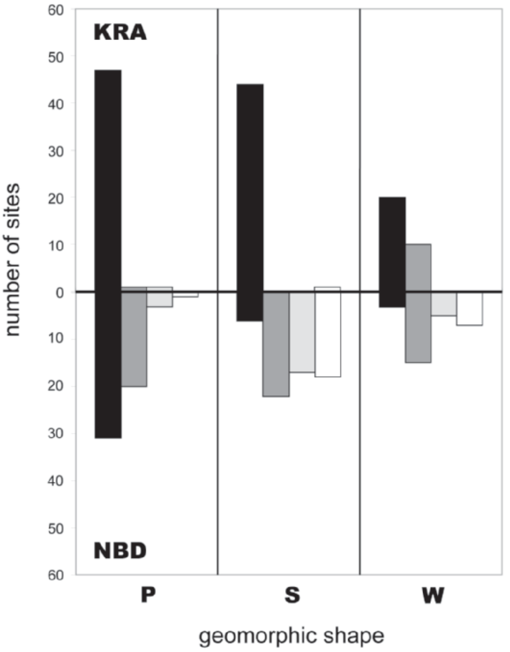

Fig. 3. Histogram showing disturbance classes for recent disturbance in Keys Ranch Area (KRA; above origin) and North Barker Dam (NBD; below origin). The geomorphic categories are pockets (P), slopes (S), and wash banks (W). Lowest disturbance sites (1, darkest shading) through highest disturbance sites (4, no shading) were ranked as described in the methods section.

were used for further pattern analysis. The software package MSVP was used to conduct principal components analysis (PCA) to determine which environmental factors in the ecosystem most clearly influenced distribution and abundance of biological soil crusts.

RESULTS

Site and Soil Characterization

Tabulation of the disturbance index suggested that the NBD sites have experienced more recent disturbance (foot traffic from recreational visitation) than the KRA sites have (Fig. 3). Pocket sites were the least affected geomorphic feature with regard to human trampling disturbance. No difference of soil stability with respect to water erosion was detected for the area. However, wash banks had a significantly higher stability than pockets and slopes (Table 1).

KRA demonstrated higher vascular plant species richness than NBD, which had higher abundance of nonnative species. Vascular plant cover did not vary significantly by specific category or total vascular cover between the 2 areas (Table 2). The wash banks did have significantly higher total vascular cover due to the increased presence of annuals (Table 2).

Physical and chemical soil properties did not vary significantly between the 2 soil depths (0–0.5 cm, 0–3 cm). Therefore, only data for surface samples (0–0.5 cm) will be reported and analyzed herein (Table 3). Total gravel content was significantly higher at NBD sites. Gravel content was highest from slope sites and lowest from wash bank sites. All together, soils on pocket and slope sites were very gravelly. Particle size distribution showed no differences based on area or geomorphology (Table 3). All soil textures could be classified as sandy loam (Schoeneberger et al. 2002).

The soil chemical properties for slope and pocket sites did not vary significantly between areas. However, significant differences occurred between wash bank sites and the other 2 geomorphic features. Wash bank pH means were about 1 unit more alkaline than pockets and slopes. Also, wash bank sites had significantly higher electrical conductivity than the other 2 geomorphic features (Table 3). Total carbon and total nitrogen showed no significant differences among areas for slope and pocket sites. However, wash bank sites showed significantly higher TC and TN values than the other geomorphic features (Table 3).

Biological Soil Crust Characterization

Biological soil crusts on soil islands in the Wonderland of Rocks contribute a mean ground cover of around 30%–50%. Lichen and moss crusts were not an important component of the ground cover in either area for all 3 geomorphic features (ground cover $\leq$3%; Table 2). Total crust cover was significantly higher in KRA due to the high incidence of algal crust. However, moss cover and mixed crust cover was significantly higher in NBD, primarily due to the relatively higher cover of these classes on the wash banks (Table 2). Bare soil was significantly higher in NBD and may represent either less surface colonized by plants and biological soil crusts or higher incidence of disturbance.

Frequency data from the largest quadrats (0.25 m^2) were used for rare categories such as lichen or moss crust and were selected for ANOVA analyses, while data from the smallest quadrats (0.0025 m^2) were used for the more

TABLE 2. Mean percent cover for scored cover classes in 2 areas of Joshua Tree National Park. Means are summarized by geomorphology. Significance probability values are reported for main effects only (study area: NBD, KRA; geomorphology: pocket, slope, wash bank). The area with the significantly higher cover value is indicated in lowercase letters following the probability value (nbd = North Barker Dam, kra = Keys Ranch Area). The geomorphic feature with the significantly highest cover value is also indicated in lowercase letters following the probability value (p = pocket, s = slope, w = wash bank).

	North Barker Dam (NBD)			Keys Ranch Area (KRA)				
Cover class	pocket	slope	wash bank	pocket	slope	wash bank	Area *P*	Geomorph. *P*
Annual	5.8	2.3	10.3	4.0	4.8	8.8	0.806	<0.001 w
Grass	1.3	0.4	0.6	0.9	0.2	0.1	0.399	0.012 p
Shrub	0.2	1.1	0.0	0.4	0.4	0.1	0.493	0.207
Total vascular	7.3	3.8	10.9	5.3	5.4	9.0	0.481	<0.001 w
Algal	25.1	24.5	28.0	32.0	32.7	52.8	<0.001 kra	0.003 w
Mixed	7.8	2.3	20.7	11.3	3.9	0.3	0.006 nbd	<0.001 pw
Lichen	1.1	0.1	0.0	0.6	0.7	0.0	0.776	0.065
Moss	1.5	0.5	2.7	0.7	0.1	0.1	0.003 nbd	0.064
Total crust	35.5	27.4	51.4	44.6	37.4	53.2	0.039 kra	<0.001 w
Plant litter	20.4	12.5	22.9	22.8	19.1	25.8	0.014 kra	0.001 w
Bare soil	0.7	4.3	4.4	0.9	1.0	1.6	0.003 nbd	0.009 sw
Gravel (2–76 mm)	59.2	70.9	23.6	55.7	57.4	29.9	0.128	<0.001 s
Rock (>76 mm)	2.4	6.3	4.0	7.1	12.3	3.9	0.034 kra	0.003 s
Other	0.3	0.1	0.3	0.8	0.7	0.2	0.135	0.483

TABLE 3. Physical and chemical characteristics for surface samples (first 0.5 cm) in 2 areas of Joshua Tree National Park. Means are summarized by geomorphology. Significance probability values are reported for main effects only (study area: NBD, KRA; geomorphology: pocket, slope, wash bank). The area with the significantly highest value for a variable is indicated in lowercase letters following the probability value (nbd = North Barker Dam, kra = Keys Ranch Area). The geomorphic feature with the significantly highest value for a variable is also indicated in lowercase letters following the probability value (p = pocket; s = slope, w = wash bank).

	North Barker Dam (NBD)			Keys Ranch Area (KRA)				
Parameter	pocket	slope	wash bank	pocket	slope	wash bank	Area *P*	Geomorph. *P*
Gravel (%)	37.3	45.0	21.3	25.7	36.5	17.2	<0.001 nbd	<0.001 s
Sand (%)	75.8	77.0	77.8	77.2	75.6	75.7	0.367	0.921
Silt (%)	12.2	11.3	10.9	8.1	9.0	11.7	0.025 nbd	0.479
Clay (%)	12.0	11.7	11.3	11.8	11.7	12.0	0.999	0.960
pH	6.5	6.5	7.3	7.1	7.1	7.8	<0.001 kra	<0.001 w
EC ($ds \cdot m^{-1}$)	0.6	0.5	4.2	0.6	0.9	1.9	0.012 nbd	<0.001 w
TC (%)	0.86	0.54	1.34	0.77	0.91	1.25	0.580	0.001 w
TN (%)	0.07	0.05	0.11	0.06	0.07	0.10	0.588	<0.001 w
C/N	11.4	11.0	11.7	11.5	11.5	11.6	0.767	0.819
Chl *a* (μg chl. *a*/g soil)	26.5	15.3	46.2	16.5	14.9	24.9	<0.001 nbd	<0.001 w

TABLE 4. Mean percent nested frequency for selected scored frequency classes in 2 areas of Joshua Tree National Park. Means are summarized by geomorphology within area. Significance probability values are reported for main effects only (study area: NBD, KRA; geomorphology: pocket, slope, wash bank). The area with significantly higher frequency is indicated in lowercase letters following the probability value (nbd = North Barker Dam, kra = Keys Ranch Area). The geomorphic feature with the significantly highest value in percent frequency is also indicated in lowercase letters following the probability value (p = pocket; s = slope, and w = wash bank). Plot sizes are in parentheses: 1 = 0.25 m^2 and 6 = 0.0025 m^2.

	North Barker Dam (NBD)			Keys Ranch Area (KRA)				
Frequency class	pocket	slope	wash bank	pocket	slope	wash bank	Area *P*	Geomorph. *P*
Algal (6)	44.5	36.5	49.2	55.1	58.0	76.1	<0.001 kra	0.046 w
Mixed (1)	62.2	22.9	78.8	61.5	36.8	18.7	0.012 nbd	<0.001 pw
Lichen (1)	25.7	8.7	0.0	29.8	22.9	0.0	0.202	<0.001 p
Moss (1)	30.4	13.3	34.7	25.7	11.6	4.3	0.028 nbd	0.030 p
Total crust (6)	49.2	40.4	74.4	68.0	61.1	76.1	0.005 kra	0.001 w

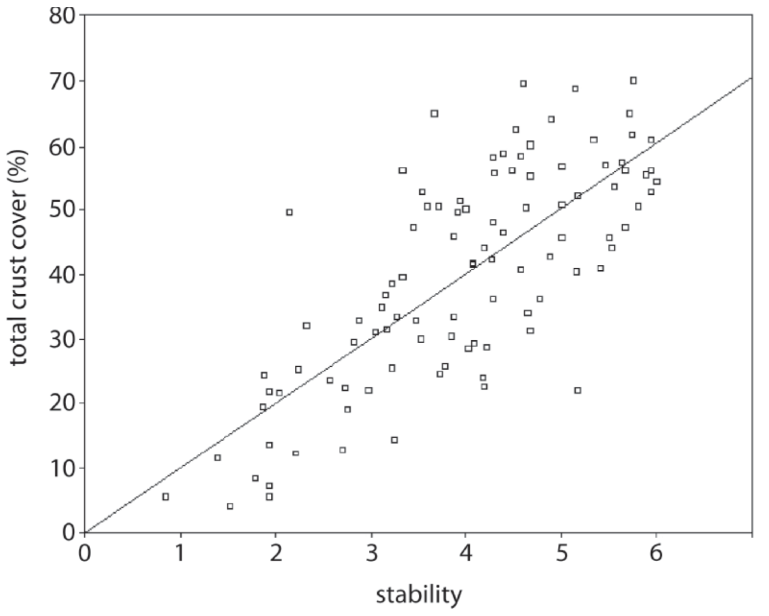

Fig. 4. Scatterplot demonstrating positive correlation of total crust and stability values revealed from 2 areas of Joshua Tree National Park. Cover values are given as percentages.

prevalent categories of algal crust and total crust. Moss and lichen crusts were significantly more frequent in pocket sites (Table 4). In KRA, algal crust and total crust were significantly more abundant than in the NBD area (Table 4).

As a photosynthetic biomass indicator, chlorophyll *a* varied significantly between the 2 areas and among the 3 geomorphic features. The highest values with ca. 46.2 μg chlorophyll *a* per g soil were recorded for the wash bank sites of NBD, followed by pockets with 26.5 μg chlorophyll *a*/g soil, and slopes with 15.3 μg chlorophyll *a*/g soil (Table 4). Chlorophyll *a* in KRA was significantly lower but showed similar patterns among the geomorphic features (Table 4).

Biometric Analyses

Percent total gravel displayed a negative correlation with soil crust cover ($R^2 = 0.37$). Soil stability and total crust cover were positively correlated with each other ($R^2 = 0.57$; Fig. 4), demonstrating the linkage between algal crust development and soil cohesion. Apart from these 2 correlations, no strong correlations with crust cover in the various categories could be detected.

Principal components analysis (PCA) was used to ordinate samples and sites with crust data (chlorophyll *a* plus cover values for algal, lichen, moss, mixed crust, and total crust cover) for all soil island sites examined. A total of 69.5% of the variability in the data could be explained with the plot (Fig. 5; Axis 1 = 42.4%, Axis 2 = 27.1%). Sites with better crust development are to the right of the origin. Slopes clustered on the negative side of axis 1 and therefore tended to have poorer crust development, while the wash banks clustered on the positive side and tended to have better algal crust development. The pockets are scattered throughout the plot, indicating that they are the most variable geomorphic feature with regard to crust development.

Differences between KRA and NBD were not conspicuous, although it appeared that the wash bank sites of NBD tended to be higher in lichen and moss cover than the KRA sites, which tended to have higher algal crust cover.

In a second PCA, samples and sites were ordinated with physical and chemical data (Fig. 6). A clear separation among the geomorphic categories was evident. A total of 55.1% of the variability in data could be explained by the first 2 axes (Axis 1 = 35.4%, Axis 2 = 19.7%). Axis 1 is positively weighted by factors associated with finer-textured soils (C, N, EC, pH, silt, and clay) and negatively weighted by sand and gravel categories. The wash banks contained the finer-textured soils, while the slopes and pockets

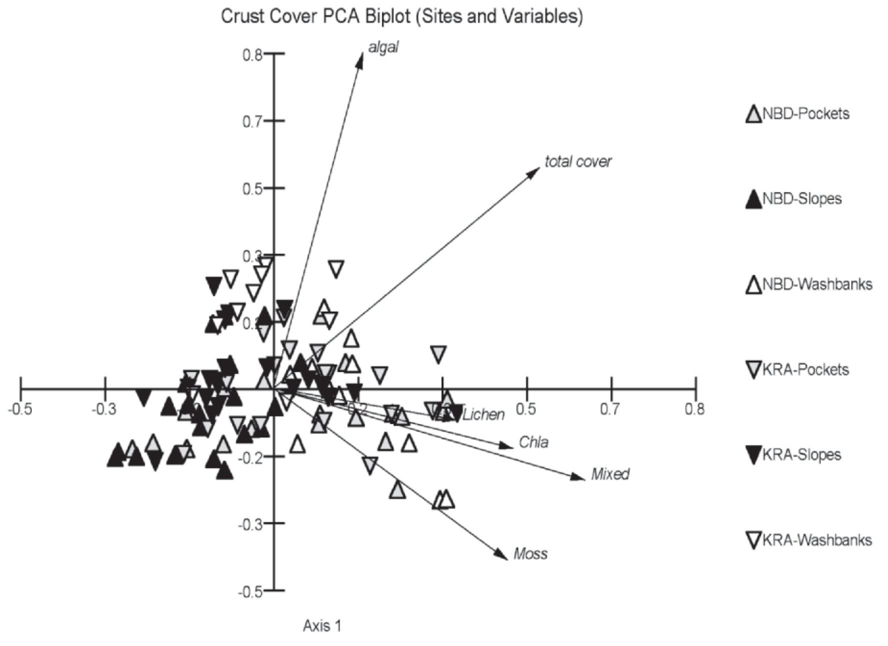

Fig. 5. PCA biplot for crust cover data. NBD = North Barker Dam, KRA = Keys Ranch Area. Factors include chlorophyll *a* in surface samples (= Chla) and the following crust categories: algal crust cover = algal, lichen crust frequency = Lichen, moss crust frequency = Moss, mixed crust cover = Mixed, and total crust cover = total cover.

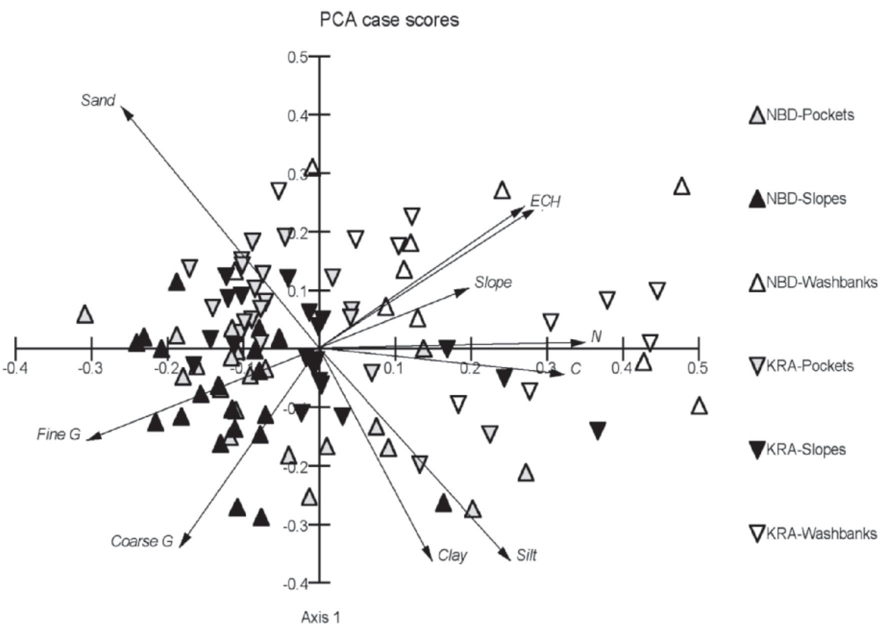

Fig. 6. PCA biplot for soil chemical and physical data from North Barker Dam (NBD) and Keys Ranch Area (KRA). C = carbon, N = nitrogen, Fine G = fine gravel, Coarse G = coarse gravel, other factors self-explanatory.

tended to be coarser textured. Fine-textured soil was positively associated with good development of crust cover, whereas coarse soil textures and high gravel contents were negatively associated. Differences between KRA and NBD samples were not evident.

DISCUSSION

Biological soil crusts of the Mojave Desert are very different in composition and form than crusts of the other desert regions of North America, reinforcing the observations made in other studies of the Mojave Desert (Johansen et al. 2001, Pietrasiak et al. 2011). Both cover and frequency data of our study demonstrate that lichen and mosses are a relatively minor component of the biological soil crusts in Joshua Tree National Park due to their very patchy and limited distribution. The biological soil crusts are primarily dominated by algae and cyanobacteria. Despite the poor development of the lichen and moss components of the crust, the crusts still increased aggregation of surface particles. A positive correlation between soil stability and crust development, as shown in previous studies (Malam Issa et al. 2001, Eldridge and Leys 2003), was verified in the soils of the Wonderland of Rocks area; soils with biological soil crust were more stable than soils without them.

We found that gravel correlates negatively with biological soil crust cover and that the gravel layer is a predominant feature in this desert ecosystem. Studies by Anderson et al. (1982b) also revealed a negative correlation with soil components >2 mm. Nevertheless, when crusts were present, gravel was often integrated into the surface feature. Based on these observations, it seems likely that the crusts may contribute to stabilizing the surface gravel layer and retaining fine soil particles in the interstices between the integrated (embedded) gravel.

In other desert areas, crust development is positively correlated with siltiness, pH and EC (Anderson et al. 1982b, Belnap 2002). The particle size of the soils in our study was not strongly correlated with total crust, although our data showed a trend for finer soils to have greater lichen and moss crust development. The lack of importance of soil texture in this study was likely because silt content was very low and soil texture did not vary significantly between sites.

PCA showed that a trend existed in which soils of higher EC tended to have better crust cover development. Higher EC values were found in the wash bank sites, which had significantly higher total crust cover development. It is difficult to determine if wash bank sites have elevated EC due to the presence of crusts or if crusts are better developed in wash banks because EC is elevated or if both occur for a different reason (compare Johansen et al. 2001).

Geomorphology apparently played a greater role in crust composition and abundance than either soil characteristics or geographic area. Geomorphic features had similar impacts on crust development in both study areas. Geomorphology likely interacts with both moisture availability and susceptibility to disturbance. For example, slopes have higher runoff and are more susceptible to erosion following trampling disturbance than either the pockets or the wash banks. Wash banks receive moisture from occasional runoff events that fill the washes but are above the primary flow, so fine soils and lack of water erosion make wash banks ideal habitats for algal and cyanobacterial growth and accumulation. Pockets are accumulation areas for both soil and water, so even disturbed soils tend to remain in place and provide favorable conditions for crust development. These intuitive interpretations were supported by the data collected in this study (Fig. 5), which consistently showed highest chlorophyll *a* along wash banks, followed by pockets, and finally by slopes (Table 3). Composition followed a different pattern, with lichen and moss components showing highest cover in the pockets, followed by the slopes (Table 4). Geomorphic differences affecting crust distribution and composition were also shown by Eldridge (1999).

The differences between KRA and NBD sites can likely be attributed to differences in disturbance regimes. The 2 sites did not differ significantly in soil characteristics, but did show marked differences in recent disturbance (Fig. 3). The slightly lower cover values of lichens and mosses in the KRA compared to the NBD area could be attributed to former grazing and animal trampling events, even though disturbance at KRA in recent years has been lower than at NBD. As shown in previous studies (Anderson et al. 1982b, Brotherson et al. 1983), animal trampling especially affects lichens and mosses. Although the ranch has not been grazed for 45 years, recovery of these fragile crusts is undoubtedly still in process. Anderson et al. (1982a) observed slow recovery of lichen and moss crusts after 18 years in a southern Great Basin study site in Utah. Johansen and St. Clair (1986) found similar timescales for lichens and mosses in more northerly Great Basin sites. But as stated earlier, recovery rates are very site specific and dependent on environmental conditions (Bowker 2007). Conditions in cold deserts (e.g., the Great Basin) differ from conditions in hot deserts (e.g., the Mojave Desert). Less precipitation or limitation of available water results in fewer mean periods of metabolic activity (see Belnap and Lange 2003). Therefore, the much drier conditions in the Mojave Desert could result in longer recovery rates for biological soil crusts (Johansen and St. Clair 1986, Evans and Johansen 1999). Stark et al. (1998) reported a growth rate of <1 mm a year for the crust moss *Syntrichia caninervis* in the Mojave Desert. Besides slow growth rates, they noted that low rates of sex expression, absence of male plants, and absence of sexual reproduction in hot deserts could slow recovery.

The significantly lower chlorophyll *a* in the KRA seems at odds with the fact that visual crust cover was higher there than at NBD. Belnap (1993) found that, even with full visual recovery of crusts (based on cover and macrophytic diversity), chlorophyll *a* values on recovery sites are often still below the level of undisturbed sites due to less photosynthetic microbiotic biomass. Hence, the crust at KRA may look more intact and score higher in cover and frequency but still may have lower photosynthetic biomass in the top centimeter of the soil. Overall, chlorophyll *a* values found in both study areas were relatively high compared to other studies of the Mojave Desert (Johansen et al. 2001, Belnap et al. 2007).

While the NBD area had a more mature crust, visual evidence of recent disturbance was much greater in this area than in the KRA (Fig. 3). Aggregate stability showed some interaction between site and geomorphology, with pockets and slopes having higher stability in KRA, while wash banks had higher stability in NBD, likely due to the increased presence of lichens and mosses in that area. The NBD area has experienced increased usage by hikers and rock climbers, and it appears that the stress of their trampling activity has put this area in a state of deterioration that could become a matter of concern for park management. In another study of Mojave Desert soils, Belnap et al. (2007) found that recent trampling disturbance decreased threshold friction velocities (i.e., the wind speed required to remove soil particles), even in areas where crust development was poor.

The level of crust recovery already evident in the KRA was more than expected. Cattle are known to have a strong negative impact on crusts, and this impact would be especially strong on a ranch. Within about 45 years of recovery from cattle grazing and about 15 years of complete recovery from all human activities, a well-established algal crust, which provides some increased soil stability, has developed. If a visible crust can develop within 45 years following intense and prolonged grazing disturbance, removing or limiting disturbance in sensitive areas may bring about recovery (Bowker 2007).

The recovery in KRA has other ramifications as well. In a recent study of distribution of biological soil crusts in the wilderness areas of Joshua Tree National Park, including areas of a more Sonoran Desert influence, Pietrasiak et al. (2011) found numerous areas lacking any crust. These areas have received far less historical disturbance (periodic, brief cattle drives along major routes; little disturbance off routes), and the disturbance was in the more distant past. Therefore, the absence of crusts in the wilderness areas is not likely due to historical disturbance events but rather to unsuitability of some soils in the Mojave Desert for crust development. Even given hundreds of years of protection from disturbance, there are some areas that will not develop crusts due to soil characteristics, microclimate, and hydrology. It appears that factors excluding crust development could be low manganese and phosphate contents, highly mobile surfaces (such as washes and open bajadas), well-developed desert pavement, very low precipitation, and high temperature (Anderson et al. 1982b, Eldridge 1996, Loppi et al. 2004). The Mojave Desert is a hot, arid region, and many crust species simply cannot prosper in the harsh conditions present in this North American desert.

This detailed study of crusts within 2 geographically limited areas of Joshua Tree National Park will serve as a valuable baseline study for monitoring changes in crust cover and development in this high-use area of the park. The Wonderland of Rocks receives the highest hiker activity in the park, because of the excellent rock-climbing opportunities in this area. We expect that the KRA area will continue to recover from historical grazing, while the NBD area will suffer further degradation of crusts as hikers continue to use it to access climbing areas. Currently, the NBD area has open access with no off-trail restrictions and few designated trails. We recommend that park managers establish a more complete trail system with appropriate signage that provides access to climbing areas while restricting off-trail trampling.

CONCLUSION

Biological soil crusts in the Little San Bernardino Mountains are dominated by algae and cyanobacteria. Individual physical and chemical variables (e.g., pH, EC, percent sand, and percent silt) have been shown to control crust in previous studies in other arid environments (compare Anderson et al. 1982b, Belnap 2002). We tested the association of these variables with Mojave Desert crust development but did not obtain strong correlations. In addition, TC and TN level could not be directly associated with crust development.

PCA revealed strong patterns according to geomorphic features (compare Eldridge 1999). PCA also showed that important factors controlling crust distribution are gravel content and coarse soil texture. This study confirmed that biological soil crusts enhance surface stability.

Given the fact that recent human trampling was implicated in a reduction of visible crust cover in this study, care should be taken to document future land use more quantitatively. The National Park Service should try to preserve the valuable resources in the Wonderland of Rocks area by establishing a trail system throughout the NBD area to prevent further crust degradation, soil loss, and loss of microbial biodiversity. Such a trail system could limit the off-trail traffic now evident.

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