

Biological Soil Crusts in a Xeric Florida Shrubland: Composition, Abundance, and Spatial Heterogeneity of Crusts with Different Disturbance Histories

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A B S T R A C T

Biological soil crusts consisting of algae, cyanobacteria, lichens, fungi, bacteria, and mosses are common in habitats where water and nutrients are limited and vascular plant cover is discontinuous. Crusts alter soil factors including water availability, nutrient content, and erosion susceptibility, and thus are likely to both directly and indirectly affect plants. To establish this link, we must first understand the crust landscape. We described the composition, abundance, and distribution of microalgae in crusts from a periodically burned, xeric Florida shrubland, with the goal of understanding the underlying variability they create for vascular plants, as well as the scale of that variability. This is the first comprehensive study of crusts in the southeastern United States, where the climate is mesic but sandy soils create xeric conditions. We found that crusts were both temporally and spatially heterogeneous in depth and species composition. For example, cyanobacteria and algae increased in abundance 10–15 years after fire and away from dominant shrubs. Chlorophyll *a* levels recovered rapidly from small-scale disturbance relative to intact crusts, but these disturbances added to crust patchiness. Plants less than 1 m apart can experience different crust environments that may alter plant fitness, plant interactions, and plant community composition.

Introduction

Soil microorganisms commonly aggregate soil particles to form biological soil crusts (also known as microbiotic,

cryptobiotic, or cryptogamic crusts), particularly in harsh environments where vascular plant distributions are patchy and water is limited [33, 19]. Microorganisms in soil crusts include eukaryotic microalgae, cyanobacteria, bacteria, fungi, lichens, and mosses [33, 19]. Polysaccharides excreted by filamentous algae and cyanobacteria, along with the living organisms themselves, bind soil particles together into a single, consolidated layer to form a crust of the first few centimeters of surface soil [4, 15].

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Soil crusts are widely thought to be ecologically important in arid ecosystems where they can change soil moisture and nutrient cycling [40, 55, 15, 33, 22]. Furthermore, nitrogen fixation by soil microbes can be a primary source of nitrogen for plants in low-nutrient desert ecosystems [21] and soil crusts can affect the germination, growth, and nutrient content of vascular plants (e.g., [44, 58, 29, 10]).

It is important to characterize the spatial distributions of organisms within crusts because of their abiotic effects on both physical and chemical soil properties and their potential influence on vascular plants. A variety of biotic and abiotic factors may contribute to spatial heterogeneity of crust organisms. Disturbance history is important because soil crusts are vulnerable to both small- and large-scale disturbances [63, 19]. Scale is also an issue—it is common to find intact and disturbed patches of soil crust occurring interspersed at a variety of scales. The relative size of disturbed patches may range from a trail of footprints, bike tires, or off-road vehicles in an otherwise intact landscape, to widely trampled or burned areas within which a few small areas of intact crust remain. Differences among crust patches in the ability to recover from disturbance may also affect their heterogeneity. Recovery time of disturbed soil crusts is variable, with estimates ranging from 1 to 100 years depending on crust type, patch size, and distance to intact crust [33, 11]. Algal crusts recover more rapidly than crusts composed primarily of lichens and mosses [36, 34, 12].

We characterized the distribution and spatial heterogeneity of species composition and abundance in photosynthetic crusts for sites with different disturbance histories in a xeric Florida shrubland. Very little is known about soil crusts in areas that have relatively mesic climates, but are xeric due to sandy soils. The crusts in these sites may be unique with respect to their more intensively studied counterparts in arid and semiarid habitats of the western United States. Our study consisted of five parts: (1) we identified the cyanobacteria and eukaryotic microalgae (including the diatoms) present in the crust; (2) we determined the distribution and degree of aggregation of these taxonomic groups across different spatial scales; (3) we analyzed species composition as a function of time since fire and shrub distance; (4) we examined the depth of soil crusts; and (5) we studied the effects of small-scale disturbance on the abundance of crust organisms as indicated by chlorophyll *a* levels. We also measured chlorophyll *a* of samples in the distribution study to see how well it re-

flected the actual abundance of microorganisms. We limited our investigation to the green algae, cyanobacteria, and diatoms in these crusts because as primary producers, they are thought to play a role in the initiation of soil crusts [15]. Additionally, soil crusts in Florida scrub are “flat” crusts that are characteristically dominated by algae and cyanobacteria rather than by lichens or mosses [33].

Methods

Study Site

This study took place in rosemary scrub sites at Archbold Biological Station, located near the southern tip of the Lake Wales Ridge in Highlands County (27°11' N latitude, 81° 21' W longitude), Florida. Florida scrub is a xeric, pyrogenic shrubland found on Plio-Pleistocene sand ridges in central peninsular Florida at elevations ranging from 36 to 67 m above sea level [1]. The climate is one of hot, wet summers and mild, dry winters. Average annual precipitation is 1331.8 mm (s.e. = 28.6 mm) with almost half this amount falling between June and August (Archbold Biological Station weather records, 1932–2000).

The present study focuses on soil crusts in the rosemary phase of sand pine scrub (i.e., “rosemary scrub” [1], in which Florida rosemary (*Ceratiola ericoides*) is the dominant shrub, with clumps of scrub oaks (*Quercus inopina*, *Q. geminata*, *Q. chapmanii*) and sand pines (*Pinus clausa*) (nomenclature follows Wunderlin [65]). The shrubs are interspersed with open gaps of various sizes where both herbaceous plants [38, 46] and extensive areas of soil crust are found. Rosemary scrub is restricted to acidic (pH 4.2 to 5.2), excessively well-drained, white sands (St. Lucie or Archbold soil types) at elevations ranging from 40 to 50 m [1]. Patches of rosemary scrub are primarily less than 1 ha in size at Archbold [1] with fire intervals of 15 to 100 years [37, 46]. For site details, see [Hawkes CV (2000), Biological soil crusts and their interactions with vascular plants in a xeric Florida shrubland. PhD Thesis, University of Pennsylvania, Philadelphia, PA, 201 pp].

The abundant soil crusts in rosemary scrub are primarily flat (i.e., lacking microtopography) with occasional dark, elevated patches. Terricolous lichens, *Cladonia* and *Cladina* spp. [49] with a green algal phycobiont, *Trebouxia* spp. [2], become numerous on top of the soil approximately 15 years after fire ([48], [Hawkes CV (2000) Biological soil crusts and their interactions with vascular plants in a xeric Florida shrubland. PhD Thesis, University of Pennsylvania, Philadelphia, PA, 201 pp]). These lichens do not seem to become physically intertwined with soil crusts and do not fix nitrogen. Mosses are rare, occurring in small patches only in long-unburned, undisturbed sites.

Crust Composition

Samples for culturing of cyanobacteria and non-diatom eukaryotic algae were collected from five rosemary scrub sites and one

sand road adjacent to rosemary scrub in July 1997. We combined and homogenized crust subsamples (1–2 cm deep) taken from 25 random positions in each site. From each composite sample, 10^{-2} dilutions were made in 0.7% saline solution and aliquots of 0.1 and 0.2 ml were spread in triplicate on two agar-solidified media: Z-8 [16] for quantification of cyanobacteria and Bold's Basal (BBM; [14]) for quantification of non-diatom eukaryotic algae. Cultures were incubated in constant light at 20–23°C until good growth had been obtained (3–6 weeks). The number of colony forming units on each plate was counted.

For the identification of cyanobacteria, wet mounts prepared directly from individual isolates on Z-8 plates were examined using an Olympus BH-2 photomicroscope with Nomarski DIC optics and photographed using Kodak PKL-135 film. Identification was made on the basis of cell and colony morphology using standard authoritative references [18, 27, 39]. Because many cyanobacteria grow poorly on artificial media, additional identifications of cyanobacteria were made directly from wet mounts of wetted soil samples incubated 48–72 h in the light.

For identification of non-diatom eukaryotic algae, individual isolates were picked into 5 mL liquid BBM and incubated for 2–4 weeks. Identification was made on the basis of life history and morphological criteria using standard authoritative references [20, 41].

Additionally, we identified cyanobacteria, green algae, and diatoms from field samples collected for study of the distribution of organisms and observed with a fluorescence microscope (described below).

Crust Distribution

Between September 1998 and April 1999, we measured the chlorophyll *a* content, soil moisture, and biovolume and density of green algae, cyanobacteria, and diatoms of crusts. Soil crusts were examined at six rosemary scrub sites with replicate sites of three postfire classes (<8, 10–15, and >30 years since fire). Samples were taken at 0, 0.5, 1, 10, and 50 m along a randomly placed transect in each site. The smaller distances (0.5 and 1 m) correspond to the sizes of individual herbaceous plant root systems [Hawkes CV (2000) Biological soil crusts and their interactions with vascular plants in a xeric Florida shrubland. PhD Thesis, University of Pennsylvania, Philadelphia, PA, 201 pp]; the larger distances (10 and 50 m) represent between-plant locations. At each distance along the transect, crusts were sampled near (0 m) and away (0.5 m) from the nearest *C. ericoides* shrub with two sterile test tubes, each pressed into the soil surface twice to a depth of 2 cm. One tube was used for analysis of chlorophyll *a* content, the other for fluorescence microscopy to determine species composition, density, and biovolume. An additional, comparable amount of crust was collected and sealed in a plastic bag for measurement of gravimetric moisture.

Samples collected for analysis of chlorophyll *a* were immediately extracted with DMSO using standard methodology [3, 53, 6, 13, 11; Hawkes CV (2000) Biological soil crusts and their interactions with vascular plants in a xeric Florida shrubland. PhD

Thesis, University of Pennsylvania, Philadelphia, PA, 201 ppl]). Chlorophyll *a* content on a per volume basis was calculated as: $\text{Chlor } a (\mu\text{g} \cdot \text{cm}^{-3}) = 27.73 \, d/v/aL$, where $d = (A_{655} - A_{750})_{\text{before acid}} - (A_{655} - A_{750})_{\text{after acid}}$, v is the extract volume, a is the volume of the crust sample, L is the length of the light path, and 26.73 is a constant accounting for the absorbance coefficient of chlorophyll *a* and a correction for acidification [3, 53, 6, 13, 11].

To characterize spatial variation in species composition, a 1-g aliquot of each sample was shaken with 10 mL of distilled water and a subsample was placed in a counting chamber of known volume ($18 \times 0.38 \times 0.1778$ mm) [60, 35]. We directly observed ten 18-mm transects for each sample using an Olympus BH-2 fluorescence microscope with a blue filter at a total magnification of 400×. Living eukaryotic algae and cyanobacteria were photographed, identified, counted, and their linear dimensions measured. Individual cell and filament volumes were calculated following the guidelines of Hillebrand et al. [30]. From these measurements, the biovolume and density of organisms in the sample were calculated.

We estimated Morista's Index (\hat{I}_m) as a measure of aggregation [32] for three groups: cyanobacteria, green algae, and diatoms. \hat{I}_m was calculated for several spatial scales by including densities of samples from increasingly greater distances along the field transects (0.5, 1, 10, and 50 m). Calculations were made separately for each time since fire. Morista's Index can range from zero to the number of samples in the study. A random distribution is indicated by $\hat{I}_m = 1$; $\hat{I}_m > 1$ indicates aggregation [32].

We analyzed the biovolume, density, and number of species in each taxonomic group (cyanobacteria, green algae, and diatoms) as a function of time since fire and distance from *C. ericoides* shrubs with multivariate ANOVA. Chlorophyll *a* as a function of time since fire and distance from shrub was also examined with ANOVA. Post-hoc comparisons were made for significant factors ($p < 0.05$) using Ryan–Einot–Gabriel–Welsch *F* tests. When data did not meet the assumptions of normality or homogeneity of variance, they were monotonically transformed as follows: ln (cyanobacteria density, diatom density), square root (green algae density, diatom biovolume), or square root and ln (chlorophyll *a*). Cyanobacteria and green algae biovolume data were normalized by ln transformation, but variances remained heterogeneous (Levene's test of equality, cyanobacteria: $F = 6.078$, green algae: $F = 7.383$, $df = 5, 42$, $p < 0.001$). Although we recognize potential inflation of the Type I error rate, we nevertheless ran the ANOVA on the transformed biovolume data because in a balanced design, our number of treatment levels and sample sizes are large enough so that the analysis should be robust to violations of its assumptions [61]. Pearson correlations among the dependent variables were also calculated, with Dunn–Šidák corrections for multiple comparisons [57].

Ordination of the crust community data was accomplished with nonmetric multidimensional scaling (NMS; [17]) for six sites, 34 species, and three environmental variables: time since fire, site, and shrub distance. We performed the NMS on both species density and biovolume data using the recommended procedures in PC-ORD [45].

Crust Depth

We measured the depth of crust consolidation in nine sites of three postfire categories (<8, 10–15, and >30 years since fire), both beneath (0 m) and 1m away from the nearest *C. ericoides* shrub ($n = 10$) in June 1997. Depth was square root transformed and analyzed as a function of time since fire and *C. ericoides* shrub distance with two-way ANOVA. Post-hoc Šidák comparisons were performed when $p < 0.05$.

The depth of photosynthetic microbes in crusts was estimated as the depth of chlorophyll *a*. We measured chlorophyll *a* in six sites in three age classes (<8, 10–15, and >30 years since fire) near and away from *C. ericoides* shrubs ($n = 4$) in January 1998. We sampled at three depths (0–1 cm, 1–2 cm, 2–3 cm) and analyzed for chlorophyll *a* as described above. A fixed model ANOVA was used to determine the dependence of chlorophyll *a* on depth, time since fire, and distance from *C. ericoides*. Post-hoc Šidák comparisons were made for significant factors ($p < 0.05$). Chlorophyll *a* data were square root and ln-transformed prior to statistical analysis.

Effects of Disturbance on Crusts

We attempted to mimic common small-scale disturbances in rosemary scrub such as trampling and digging in the context of site fire history. Between September and October 1998, 1200 1-m² plots were established at random points near and away from *C. ericoides* shrubs in 11 sites of three postfire classes (<8, 10–15, and >30 years since fire). Each plot was assigned to one of three soil crust treatments: intact, disturbed, or removed. In disturbed plots, crusts were crushed with a trowel and raked until no aggregation remained. Crusts in removed plots were dug to a depth of approximately 4 cm and removed. Intact crusts were left untouched. We measured chlorophyll *a* and gravimetric moisture in each plot between March and April 1999. ANOVA was used to assess the effects of site age, distance to shrub, and crust disturbance treatment on chlorophyll *a* content.

To test whether crust recovery from disturbance was location-dependent, we analyzed a subset of the disturbance plots for spatial autocorrelation of chlorophyll *a*. We determined spatial locations of 340 randomly selected plots from 3 sites with GPS and used Mantel tests to examine the association between chlorophyll *a* and the reciprocal of distance within each site [43, 26]. Standardized Mantel statistics were calculated in PC-ORD [45] with Sorenson's distances for the matrices; associated p -values were calculated with Monte Carlo randomization ($n = 1000$ runs).

Results

Crust Composition

Approximately 35 morphotypes of cyanobacteria and eukaryotic algae were observed (Tables 1, 2), with 15 species confirmed through culturing (Table 1). Only two

Table 1. Distribution of taxa found through culturing at five sites in three categories of time since fire (TSF)^a

Species	R	TSF <8 yrs		TSF 10–15 yrs	TSF >30 yrs	
		6	49	90	93	59
Cyanobacteria						
<i>Microcoleus</i> sp.	0	0	0	0	0	+
<i>Schizothrix calcicola</i>	0	0	+	0	0	0
Chlorophyta						
<i>Chlorella vulgaris</i>	0	0	+	0	0	0
<i>Chlorella</i> sp.	+	0	+	0	0	0
<i>Chlorococcum</i> <i>pinguideum</i>	0	+	0	+	+	0
<i>Chlorococcum</i> sp.	0	0	0	0	+	0
<i>Cylindrocystis brebisonii</i> var. <i>deserti</i>	0	0	+	0	0	0
<i>Elakatothrix obtusa</i>	+	+	+	0	0	+
<i>Ellipsoidion oocystoides</i>	0	0	0	+	0	0
<i>Ettlia</i> sp.	+	0	0	0	+	+
<i>Klebsormidium flaccidum</i>	+	+	+	+	0	+
<i>Muriella decolor</i>	0	0	+	0	0	0
<i>Stichococcus bacillaris</i>	+	+	+	+	+	+
<i>Tetradasmus petkoffii</i>	0	0	+	0	0	+
Xanthophyceae						
<i>Monodus coccomyxa</i>	+	+	+	+	+	+
Total Density (number/g soil × 10 ³)	0.6	16	3	18	17	2.5

^a Site “R” is a frequently disturbed sand road adjacent to site 49 included for comparison. Multiple isolates of the same taxon were recovered from most sites.

species of cyanobacteria were cultured, though 14 species were observed under the fluorescence microscope, as were three species of diatoms. Between five and 10 species were isolated from each site. From the culturing data, the crusts appear to differ slightly in composition and abundance across sites. For example, sites 49 and 59 had more diverse, lower density crusts, whereas sites 6, 90, and 93 had crusts of average diversity and high density. Surprisingly, six species were cultured from the highly disturbed sand roadside, though none were unique. Density on the roadside, however, was only one-thirtieth to one-fourth that of the scrub sites. As expected, the more extensive fluorescence microscopy data paint a different portrait of the crusts, with 27–31 species in each site and higher densities.

Crust Distribution

The concentration of all photosynthetic microbes determined by fluorescence microscopy ranged from 4.93×10^3 to 1.46×10^5 cells/g soil. Biovolume of both cyanobacteria and green algae was significantly affected by time since fire, distance to *C. ericoides* shrubs, and their interaction (Table 3). Because the homogeneity of variance criterion

Table 2. Density (number per g soil) of taxa (morphotypes) found in six sites in three since fire (TSF) classes; measurements made with fluorescence microscopy

	TSF <8 yrs		TSF 10–15 yrs		TSF >30 yrs	
	42	49	91	95	60	61
Cyanobacteria						
<i>Chroococcus minor</i>	32,880.7	18,084.4	3,699.1	3,699.1	86,928.3	8,631.2
<i>Chroococcus turgidus</i>	0	0	1,849.5	1,438.5	205.5	2,671.6
<i>Lyngbya aerugineo-caerulea</i>	1,849.5	1,233.0	205.5	205.5	411.0	8,836.7
<i>Microcoleus vaginatus</i>	0	0	5,137.6	3,082.6	411.0	3,493.6
<i>Microcystis</i> sp.	1,027.5	1,233.0	205.5	822.0	2,466.1	205.5
<i>Nodularia spumigena</i>	67,199.9	411.0	16,234.8	66,172.4	1,849.5	616.5
<i>Nostoc</i> sp.	2,877.1	411.0	3,699.1	1,438.5	2,055.0	6,165.1
<i>Oscillatoria</i> sp.	5,137.6	411.0	1,233.0	4,110.1	1,233.0	3904.6
<i>Phormidium viscosum</i>	23,838.5	2,055.0	8,014.7	10,069.7	1,027.5	10,891.7
<i>Schizothrix arenaria</i>	6,370.6	411.0	15,207.3	2,055.0	411.0	23,016.5
<i>Schizothrix calcicola</i>	1,644.0	10,891.7	4,932.1	13,152.3	1,438.5	16,029.3
<i>Scytonema</i> sp.	822.0	3,082.6	6,165.1	1,233.0	205.5	15,207.3
<i>Synechococcus aeruginosa</i>	11,508.2	1,644.0	6,781.6	2,260.6	9658.7	3,699.1
Unknown coccoid	12,946.7	4,521.1	40,073.3	30,825.6	21,7218.0	39,045.8
Chlorophyta						
<i>Chlorella</i> sp. ^a	0	123,302.5	1,644.0	11,097.2	9,864.2	3,699.1
<i>Chlorococcum pinguidium</i>	616.5	822.0	0	0	0	0
<i>Cylindrocistus brebissonii</i> var. <i>deserti</i>	1849.5	205.5	2,466.1	1,233.0	1,849.5	411.0
<i>Diplosphaera</i> sp.	616.5	3,288.1	1,027.5	10,275.2	205.0	411.0
<i>Elakatothrix obtusa</i>	2,466.1	822.0	0	0	0	0
<i>Ellipsoidion oocystoides</i>	205.5	2,260.6	822.0	4,110.1	1,644.0	205.5
<i>Ettlia</i> sp.	0	2,055.0	0	411.0	1,438.5	205.5
<i>Euastrum</i> sp.	0	0	411.0	0	205.5	822.0
<i>Klebsormidium flaccidum</i>	42,744.9	15,412.8	82,612.7	18,495.4	0	411.0
<i>Klebsormidium montanum</i>	23,427.5	2,466.1	26,715.6	15,001.8	616.5	0
<i>Monoraphidium</i> spp.	205.5	0	205.5	0	0	1,233.0
<i>Stichococcus bacillaris</i>	1,027.5	205.5	0	0	0	205.5
<i>Tetrademus</i> sp.	2,055.0	2,466.1	3,082.7	2,466.1	616.5	4,521.1
Unknown coccoid 1	12,330.3	28,154.1	17,673.4	12,124.8	10,891.7	25,071.5
Unknown filament 1	11,302.7	7,398.6	2,877.1	6,987.1	0	0
Unknown filament 2	616.5	2,466.1	1,233.0	2,055.0	411.0	205.5
Xanthophyceae						
<i>Monodus coccomyxa</i>	4,110.1	205.5	0	0	1,027.5	205.5
Bacillariophyceae						
<i>Hantzschia amphioxys</i>	411.0	2,466.1	2,260.6	1,438.5	2,260.6	2,671.6
<i>Pinnularia borealis</i>	8,014.7	4,726.6	1,233.0	2,877.1	1,233.0	3,493.6
Unknown diatom 1	616.5	1,027.5	411.0	0	205.5	1,644.0

^a The *Chlorella* sp. group includes other single-celled green algae, including *Trebouxia* sp., which could not be distinguished.

was not met, this is likely due in part to an effect of time since fire and shrub distance on the variability in biovolume of cyanobacteria and green algae. Indeed, for these two taxonomic groups both the mean and variance of biovolume peaked in sites of 10–15 years postfire and away from shrubs (Fig. 1). Green algae and cyanobacteria were also most dense away from shrubs in intermediate-aged sites (Fig. 1). Diatoms showed no consistent pattern with time since fire, but were more abundant away from shrubs than at the shrub edge (Fig. 1). The density, biovolume, and number of species were positively correlated within each taxonomic group, and some measures were

positively correlated between groups [Hawkes CV (2000) Biological soil crusts and their interactions with vascular plants in a xeric Florida shrubland. PhD Thesis, University of Pennsylvania, Philadelphia, PA, 201 pp].

The distributions of cyanobacteria, green algae, and diatoms were aggregated at all scales observed in this study. Comparisons of increasingly greater sampling distances revealed larger patches of species clumped together in the still larger landscape (Fig. 2). The degree of aggregation was greatest and most variable when samples were only 0.5 m apart for cyanobacteria and green algae, but did not change for diatoms across spatial scales.

Table 3. Results of a multivariate, fixed-model ANOVA for biovolume, density, and number of species of cyanobacteria, green algae, and diatoms as a function of time since last fire (TSF) and distance to *C. ericoides* shrubs (Shrub)^a

Source	df	Cyanobacteria			Green Algae			Diatoms			Wilks' λ
		Volume (1.457)	Density (2.785)	Num (7.964)	Volume (0.481)	Density (2372.00)	Num (5.244)	Volume (0.0004)	Density (7.492)	Num (1.440)	
TSF	2	17.305	2.118	1.154	21.129	9.035	4.159	2.065	0.649	2.126	0.132
Shrub	1	17.257	5.960	7.628	8.967	13.798	9.153	7.151	3.595	14.810	0.456
TSF \times Shrub	2	4.493	0.774	0.337	9.967	2.813	1.085	0.838	0.511	0.014	0.430

^a *F*-Ratios, degrees of freedom, and the multivariate Wilks' Lambda are reported; the MS error is shown in parentheses under each column head. Boldface type indicates $p < 0.05$.

Nonmetric multidimensional scaling grouped both density and biovolume samples by time since fire in a manner consistent with ANOVA results (Fig. 3). For density, Axis 1 was ordered along a gradient of longer to shorter time since fire with the exception of a single sample (site 42, <8 years postfire), which grouped with the long-unburned sites (Fig. 3A). Axis 2 appears to segregate the density of samples by species: mostly cyanobacteria less than zero, mostly green algae greater than zero (Fig. 3A). For biovolume, Axis 1 separated sites of 10–15 years postfire from the remaining sites corresponding to the observed peak in biovolume of crust organisms for sites in that age class (Fig. 3B). Additionally, most of the single-celled green algae cluster greater than zero along Axis 1 (Fig. 3B). Samples and species were clustered near zero along Axis 2 of the biovolume ordination.

Chlorophyll *a* measurements were generally uncorrelated with the biovolume, density, or number of cyanobacteria, green algae, or diatoms found in adjacent samples [Hawkes CV (2000) Biological soil crusts and their interactions with vascular plants in a xeric Florida shrubland. PhD Thesis, University of Pennsylvania, Philadelphia, PA, 201 pp]. Chlorophyll *a* levels decreased with time since fire ($F_{2,4} = 7.696$, MS = 0.190, $p = 0.001$); sites 10–15 and >30 years postfire had significantly lower chlorophyll *a* levels than sites <8 years since fire. Levels of chlorophyll *a* were the same near and away from *C. ericoides* shrubs ($F_{1,4} = 0.645$, MS = 0.016, $p = 0.426$) and there was no interaction of time since fire with shrub distance ($F_{2,4} = 0.884$, MS = 0.022, $p = 0.421$). Soil moisture was significantly positively correlated with chlorophyll *a* content (Spearman's rho = 0.563, $p < 0.001$; range 0.0006 to 0.1014 g water/g dry weight soil).

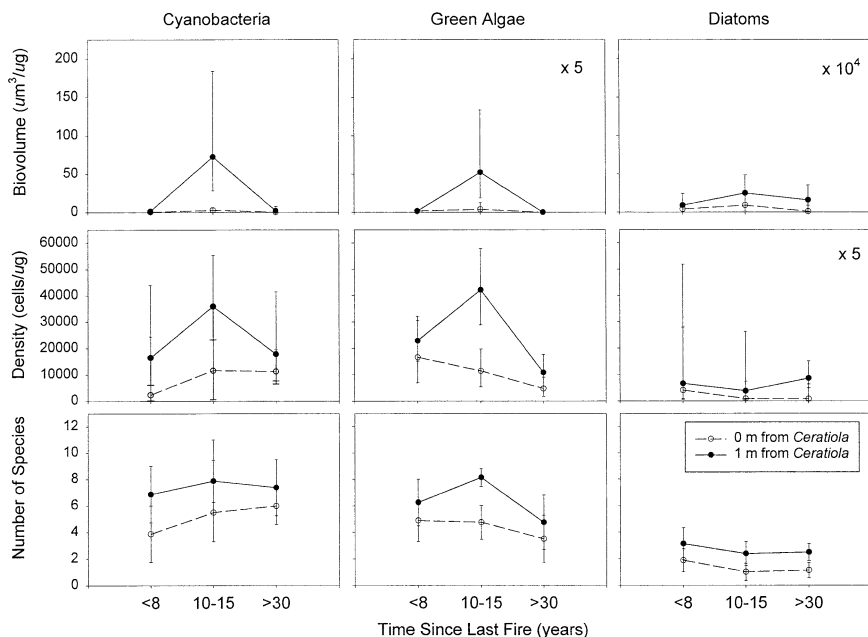


Fig. 1. Biovolume, density, and number of cyanobacteria, green algae, and diatoms as a function of time since fire and distance to *C. ericoides* shrubs (0 and 1 m from the shrub edge) ($n = 8$).

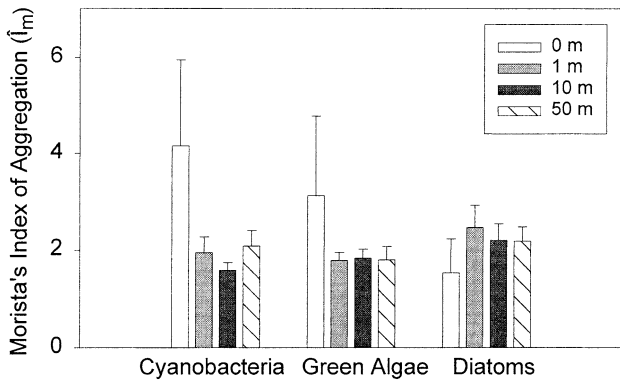


Fig. 2. Morista's Index, \hat{I}_m , is greater than 1 for every species and distance group, indicating aggregated distributions at all scales. There is greater variability in \hat{I}_m of cyanobacteria and green algae for adjacent samples (0 m). Bars are 1 standard error; averages are calculated across time-since-fire classes.

Crust Depth

The depth of aggregated soil particles ranged from approximately 0 to 1 cm, but most crusts were less than 6 mm thick (Fig. 4). Crust depth differed across time since fire ($F_{2,84} = 4.788$, $MS = 2.135$, $p = 0.011$); in long-unburned sites crusts were thicker than in young sites (Fig. 4). Though the main effect of shrub distance was not significant ($F_{1,84} = 0.087$, $MS = 0.039$, $p = 0.768$), there was a significant interaction of shrub distance and time since fire for crust depth ($F_{2,84} = 3.947$, $MS = 1.760$, $p = 0.023$). Crust aggregation was significantly deeper at the drip line than at 1 m from *C. ericoides* shrubs only in sites of intermediate age (Fig. 4).

Chlorophyll *a* levels were significantly different across sample depths (Table 4), gradually decreasing from 0 to 3 cm (Fig. 5). More chlorophyll *a* was present from 0 to 1 cm deep than from 2 to 3 cm, though intermediate depths of 1–2 cm did not differ significantly from either of these (Fig. 5). The overall pattern of chlorophyll *a* with site age was equivalent to that observed in the study of crust distribution (Table 4): chlorophyll *a* content decreased with time since fire, but in this case sites of intermediate age were not significantly different from sites <8 and >30 years since fire. Shrubs had no effect on chlorophyll *a* at any depth (Table 4).

Effects of Disturbance on Crusts

After 6 months, chlorophyll *a* in removed plots was significantly lower than in intact and disturbed plots, which

did not differ (Table 5, Fig. 6). Chlorophyll *a* also significantly decreased in experimental plots as time since fire increased (Table 5) and was unaffected by shrub distance, consistent with observations in the composition and depth studies. Soil moisture was significantly correlated with chlorophyll *a* levels in the plots (Spearman's $\rho = 0.275$, $p < 0.001$). Chlorophyll *a* measurements were not spatially autocorrelated (site 49: $r = 0.0001$, $p = 0.498$; site 95: $r = 0.0195$, $p = 0.065$; site 60: $r = -0.0167$, $p = 0.224$).

Methodological Considerations

The amount of chlorophyll *a* in the soil is generally an efficient and reliable estimation of the abundance of all photosynthetic organisms [59, 12]. In contrast to findings of other studies (e.g., [8]), however, our measurements of chlorophyll *a* did not always correspond to organism abundance. Chlorophyll *a* extraction with DMSO does not separate lichen phycobionts, photosynthetic bacteria, and algal resting stages (all of which were not otherwise measured in this study) from active, free-living soil crust algae [33]. Resting stages in particular are likely to be an important component of Florida crusts. Recent observations support this hypothesis. After heavy rainfalls, bright green blooms of algae rapidly formed both near shrubs and in the open, whereas during severe droughts few living algae were found (Hawkes, personal observation). It may also be that not all organisms survived from sampling to microscopy.

Discussion

We found a wide array of soil algae, cyanobacteria, and diatoms in rosemary scrub crusts, at densities similar to those reported for soil crusts in the southwestern United States (3.3×10^2 – 1.1×10^6 cells/g soil, [24]). Studies of soil crust composition in northern and central Florida have also found abundant cyanobacteria and algae [56, 50], but only partial overlap with the species found here. Interestingly, rosemary scrub crusts do share some species with geographically distant regions, including Baja California, Mexico [25]. It is of particular interest that two recently identified species, *Cylindrocystis brebisonii* and *Elakatothrix obtusa*, are present in both the Florida and Baja sites. To date, these species (as well as the genus *Tetrademus*) have not been recovered in extensively studied sites from Utah, California, Arizona, or New Mexico (Flechtner,

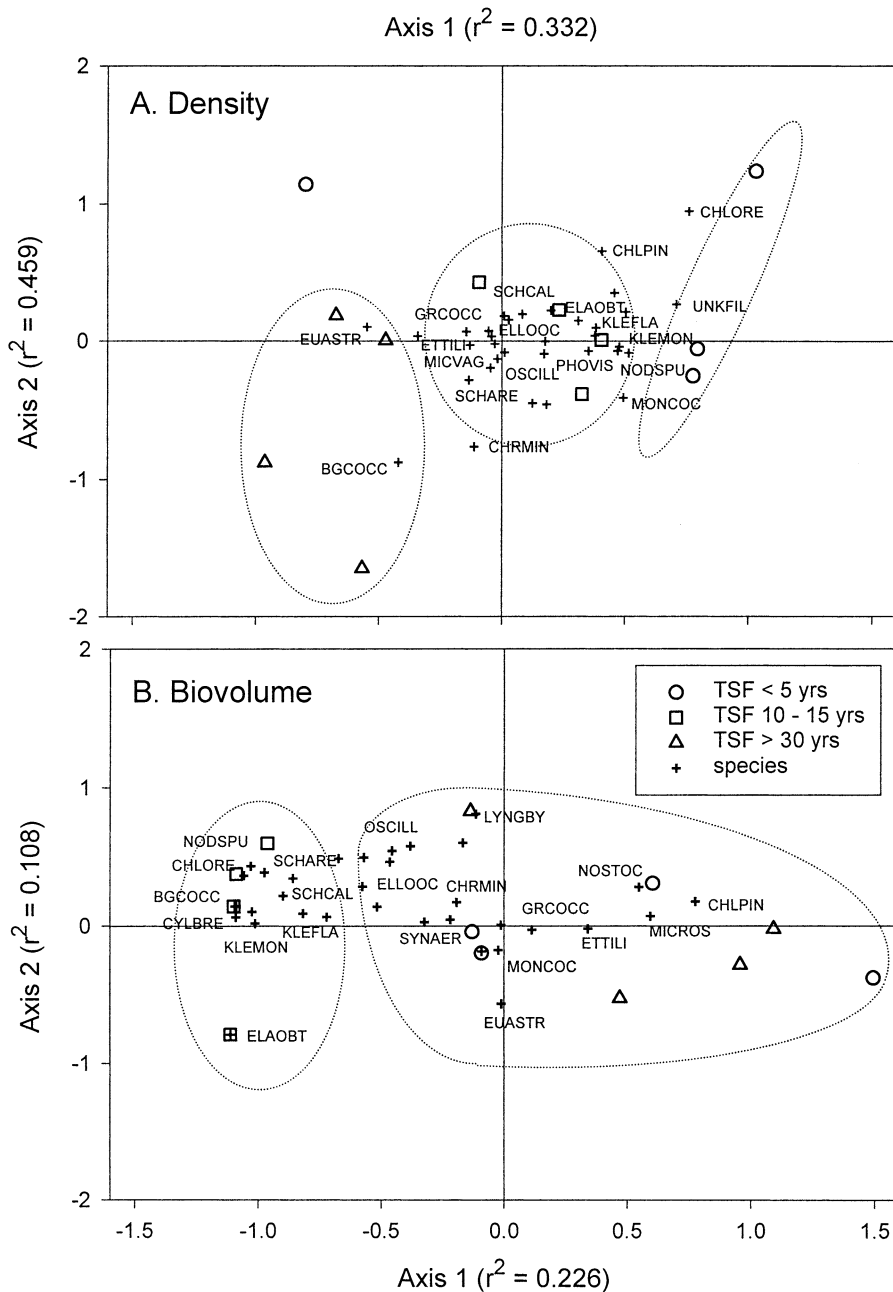


Fig. 3. Nonmetric multidimensional scaling ordination of the density (A) and biovolume (B) of samples and species. In (A), Axis 1 is consistent with a time since fire gradient. In (B), Axis 1 distinguishes sites of 10–15 years postfire. Average stress was 13.37 in (A) and 11.31 in (B). Species names are abbreviated as follows: when identified to species level, abbreviations contain the first three letters of the genus name followed by the first three letters of the specific epithet; when only identified to genus or morphotype, abbreviations consist of the first six letters of the genus or morphotype name. See Table 2 for full names.

unpublished data). The species similarity of the Florida and Baja sites may reflect present-day dispersal, similar environmental tolerances, and/or historical migrations during glaciation events [42].

Spatial variation of crust organisms was quite high, with aggregation evident at all spatial scales. Other studies have also found considerable spatial microheterogeneity, with adjacent samples as likely to contain a unique clump of species as samples more than 10 meters apart [28, 64]. The observed clumping is likely caused by a variety of factors, but in part is a result of different crust patches

being in various stages of recovery from both large- and small-scale disturbance events and at different distances from shrubs.

Little is known about how shrubs influence the distribution of photosynthetic crust organisms in shrublands where soil crusts are common [33]. In rosemary scrub, the composition and spatial distribution of green algae, cyanobacteria, and diatoms were consistently less near *C. ericoides* shrubs. Allelopathy may be the cause. Natural leachates from leaves and litter of *C. ericoides* reduce seed germination of herbs in scrub [31] and decrease growth

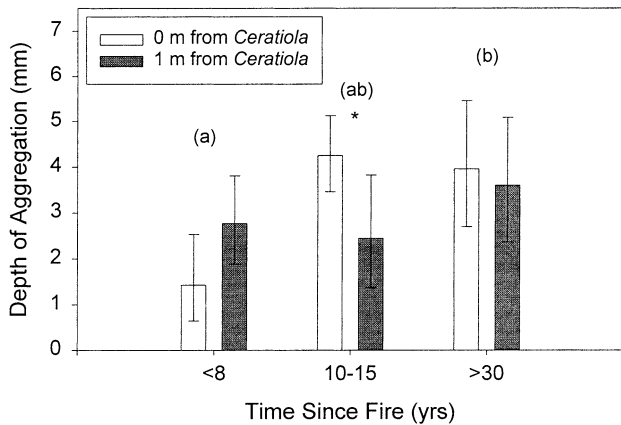


Fig. 4. The depth of soil crust aggregation was affected by both time since fire and the interaction of time since fire with distance to *C. ericoides* shrubs. Crust thickness increased with time since fire. Crusts were only significantly thicker near compared to away from shrubs in sites 10–15 years postfire. Bars are asymmetric 95% confidence intervals, $n = 15$ replicates per shrub distance. Letters indicate significant differences among time since fire classes; asterisks indicate significant differences between the 0 and 1 m shrub distances.

and survival of grasses from adjacent sandhill communities [52, 23]; crust algae may be similarly affected. In the Great Basin Desert, allelopathy by *Atriplex* and *Artemisia* shrubs is also suspected of decreasing the abundance of cyanobacteria as well as their ability to fix nitrogen [54, 55]. Other studies have found that heterotrophic microbes are more abundant near shrubs (e.g., [5, 62]), and these may also affect algal distributions.

Fire had a dramatic effect on the relative abundance of cyanobacteria and eukaryotic microalgae in rosemary scrub soil crusts. In general, abundance declined immediately postfire, peaked 10–15 years after fire, and declined again thereafter. Similar patterns are observed for plants

Table 4. Results of a three-way, fixed-model ANOVA for chlorophyll *a* as a function of time since last fire (TSF), distance to *C. ericoides* shrub, and soil depth in the study of crust depth^a

Source	df	MS	<i>F</i>	<i>p</i>
TSF	2	0.118	3.166	0.046
Shrub distance	1	0.045	1.220	0.272
Depth	2	0.242	6.471	0.002
TSF × shrub distance	2	0.098	2.614	0.077
TSF × depth	4	0.069	1.846	0.125
Depth × shrub distance	2	0.023	0.616	0.542
TSF × shrub distance × depth	4	0.014	0.382	0.821
Error	118	0.037		

^a Boldface type indicates $p < 0.05$.

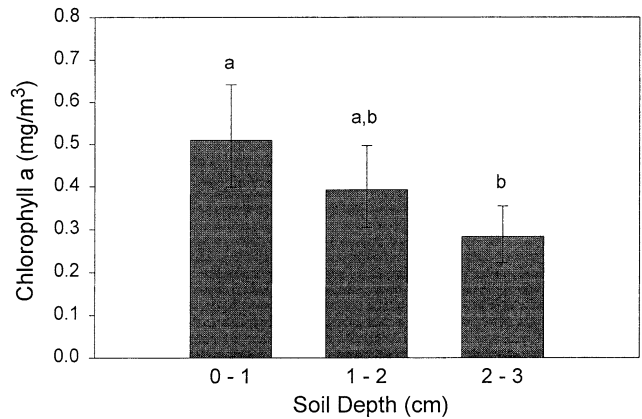


Fig. 5. Chlorophyll *a* is lower at soil depths of 2–3 cm than in the uppermost soil layer. Bars are asymmetric 95% confidence intervals. Sample sizes are $n = 48, 48, 40$ for depths 0–1, 1–2, and 2–3, respectively. Different letters represent significant differences.

and may be caused by the same mechanisms, i.e., the need to disperse back into the site after being killed by fire together with increased shrub size and decreased space in long-unburned areas [38, 47, 51].

Fire causes large-scale destruction of soil crusts in other systems. We found that species composition generally does not change after fire, but the abundance of organisms is significantly reduced; similar patterns have been observed by other investigators [34]. Johansen [33] reports that the amount of crust destruction depends on the intensity and patchiness of the fire. Fires in rosemary scrub are typically patchy because of sparse and irregular distributions of available fuels, particularly in gaps [46], which may explain the variability we observed in the abundance of cyanobacteria within fire classes.

Table 5. Results of a three-way, fixed-model ANOVA for chlorophyll *a* as a function of time since last fire (TSF), *C. ericoides* shrub distance, and soil disturbance treatment in the small-scale plots of the disturbance experiment^a

Source	df	MS	<i>F</i>	<i>p</i>
TSF	2	3.039	111.652	0.000
Shrub distance	1	0.042	1.557	0.212
Disturbance	2	0.099	3.621	0.027
TSF × shrub distance	2	0.017	0.611	0.543
TSF × disturbance	4	0.023	0.836	0.503
Shrub distance × disturbance	2	0.030	1.087	0.338
TSF × shrub distance × disturbance	4	0.058	2.148	0.073
Error	1172	0.023		

^a Boldface type indicates $p < 0.05$.

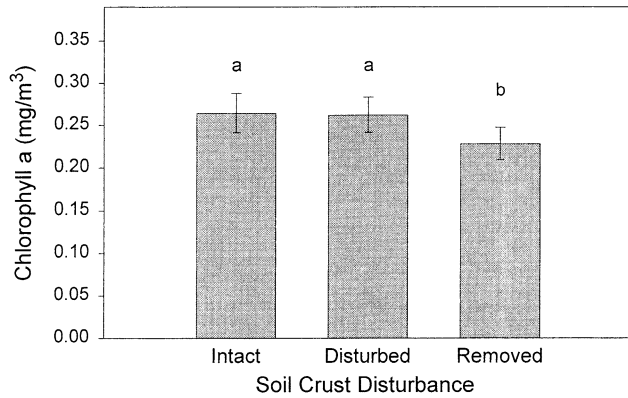


Fig. 6. Experimental disturbance treatments resulted in slightly lower chlorophyll *a* levels in removed plots compared to intact plots. Disturbed plots did not differ from either of the other treatments. Bars are asymmetric 95% confidence intervals. Different letters represent significant differences. Sample sizes are $n = 391$, 396 , and 403 for intact, disturbed, and removed plots, respectively (some plots were lost to animal disturbance).

Effects of small-scale disturbance and removal on the abundance of photosynthetic microorganisms in crusts were minimal relative to the effects of fire in rosemary scrub. Complete removal of soil crusts slightly reduced chlorophyll *a* levels 6 months after treatment, whereas small-scale mechanical disturbance had no measured effect. Disturbance of crusts in a desert system produced similar results: mechanical treatments did not significantly reduce chlorophyll *a* levels as long as crusts were left in place after disturbance [11, 7]. Crust removal presumably removes the inoculum from which crusts could otherwise recover.

Crust recovery depends on proximity to intact crusts and moisture availability [33]. We noted, however, that the spatial location of any given plot within a site in this study had no effect on chlorophyll *a* at scales of 1 m or greater. Soil moisture was significantly positively correlated with chlorophyll *a* levels. In addition, precipitation at the start of the disturbance study was far greater than the 68-year average winter rainfall: 538.25 mm compared to 157.20 ± 11.68 mm (± 1 se; Archbold Biological Station Weather Records). The increased moisture may have facilitated rapid recovery of microorganisms in crusts after disturbance through both increased growth and dispersal.

Although chlorophyll *a* levels in crusts rebound rapidly from small-scale mechanical disturbance in Florida's rosemary scrub, other crust characteristics may not recover as quickly. Species composition and evenness, for example, may be altered compared with intact crusts. The depth of crust aggregation, which increases with site age,

may be disrupted by small-scale disturbances such as animal activity. In other studies, Belnap and co-workers [11, 9] have shown that burning, mechanical disturbance, and removal of crusts dominated by both cyanobacteria and lichens dramatically reduces their ability to fix nitrogen, and this ability recovers far more slowly than chlorophyll *a* levels. In rosemary scrub, nitrogenase activity in crusts is very low in areas where the crust has been disturbed by animals and in sites <8 years after fire, but increases dramatically 10–15 and >30 years postfire [Hawkes CV (2000) Biological soil crusts and their interactions with vascular plants in a xeric Florida shrubland. PhD Thesis, University of Pennsylvania, Philadelphia, PA, 201 pp].

Overall, our findings show that soil crusts in Florida scrub are patchy and that individual vascular plants less than 1 m apart will experience differences in crust composition, biomass, and depth. Four herbaceous species in this system had an average lateral root spread of 51 cm in radius in the top 10 cm of soil [Hawkes CV (2000) Biological soil crusts and their interactions with vascular plants in a xeric Florida shrubland. PhD Thesis, University of Pennsylvania, Philadelphia, PA, 201 pp], and these species may encounter very different crust types across this distance. Because crust disturbance and different groups of crust species affect soil moisture and nitrogen differently, variation in crusts is likely to alter individual plant success, plant–plant interactions, and plant community structure.

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