Cambridge Prisms: Drylands

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Two distinct restoration approaches boost biocrust development in a post-fire, degraded dryland

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Research Article

Cite this article: Olney D, Rowe HI, Griffen K, Antoninka A and Bowker M (2026). Two distinct restoration approaches boost biocrust development in a post-fire, degraded dryland. *Cambridge Prisms: Drylands*, **3**, e40, 1–11 https://doi.org/10.1017/dry.2026.10054

Received: 14 April 2026 UTC
Revised: 24 September 2026 UTC
Accepted: 29 September 2026 UTC

Keywords:
biocrust; erosion; soil stability; Sonoran Desert; arid

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Abstract

Non-native grass invasion, human ignitions and expanding land use pressures in the Sonoran Desert, result in loss of vegetation, destabilized soils and slow ecosystem recovery. Biological soil crusts (biocrusts) – thin, coherent soil surface layers, created and inhabited by biota such as cyanobacteria, lichens and mosses – play a critical role in stabilizing soils and supporting ecosystem resilience, yet their potential as active restoration catalysts in post-fire drylands remains underexplored. This study evaluated two biocrust restoration strategies at a fire-affected site in the Tonto National Forest: application of intact strips of farmed biocrusts (sods) and dispersal of gel capsules containing biocrust material, native seeds and diatomaceous earth. Late-successional biocrust cover was eight-fold higher on sod treatments compared to the control and soil stability also increased nearby sods. Capsule treatments produced over 3x higher late-successional biocrust cover than controls in the last season. Seeded plots also supported successful seedling establishment of *Baileya multiradiata.* Together, these results demonstrate that cultivated biocrust applications can accelerate biocrust recovery, especially for late-successional taxa and increased soil stability in post-fire desert landscapes, offering a nature-based solution to reduce dryland degradation.

Impact statement

Wildfires are becoming more frequent and destructive across the world's dryland regions, increasing bare ground, triggering erosion, with recovery occurring at decadal scales. In desert ecosystems like the Sonoran Desert, this problem is compounded by invasive grasses and growing human pressures – and many native plants are not fire-adapted, prolonging recovery. The result is a cycle of degradation that threatens water quality, soil health, wildlife habitat and the communities that depend on these landscapes. This research offers a practical, nature-based path forward. By testing two innovative restoration techniques using biological soil crusts – living communities of cyanobacteria, lichens and mosses that form a protective layer on the soil surface – this study demonstrates that burned, eroded desert soils can be actively restored, rather than left to recover on their own timescale. Conducted in the Tonto National Forest in Arizona, the findings show that applying cultivated biocrust material – either as living sods placed across erosion-prone areas or as seed-and-biocrust capsules – measurably increases biocrust recovery, and sods also resulted in stabilizing soils. The implications reach far beyond Arizona. Dryland ecosystems cover roughly 40% of the Earth's land surface and are home to over two billion people. As climate change drives more frequent fire events globally, scalable and low-impact restoration tools are urgently needed. Biocrust restoration represents exactly that – an ecologically grounded strategy that land managers, conservation practitioners and policymakers can deploy across arid regions worldwide to rebuild soil health, protect watersheds and strengthen ecosystem resilience in the face of changing fire regimes and climate.

Introduction

Land degradation in drylands is accelerating worldwide due to climate change and land-use change (Prăvălie, 2016). Wildfire is becoming a new driver due to highly flammable invasive annual plants which enhance fuel connectivity (Fusco et al., 2019; Wilder et al. 2021). Resultant fires accelerate the loss of native species, increase soil erosion and affect downslope water quality (Balch et al., 2013; Wilder et al. 2021). Efforts to stabilize soils in disturbed desert landscapes are often unsuccessful for a variety of reasons. Seeding and planting restoration success is generally poor due to low and variable precipitation and active soil erosion (Abella et al., 2009; Rowe et al., 2022). Interventions are often implemented outside the optimal timeframe, and such delays can reduce their ability to prevent early soil loss and to support vegetation recovery (Gómez-Rey and

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González-Prieto, 2014). These challenges highlight the need for alternative restoration strategies that enhance native plant establishment and directly and rapidly enhance soil stability and function, even under low-precipitation conditions. Biocrust communities offer a promising tool for reducing erosion in arid regions (Zhao et al., 2016).

Biological soil crusts (biocrusts) are thin, stable soil surface layers created by cyanobacteria, lichens, mosses, fungi and other microorganisms (Weber et al., 2022). This living skin over soil surfaces is crucial in stabilizing soils, regulating hydrology and enhancing nutrient cycling in drylands (Bowker et al., 2008; Delgado-Baquerizo et al., 2013; Eldridge et al., 2020). Biocrusts cover approximately 12% of Earth's terrestrial surface and about 30% of drylands (Rodriguez-Caballero et al., 2018). However, disturbances including wildfires and other human activities can reduce biocrust cover, increase soil erosion and exacerbate ecosystem degradation (Bowker et al., 2004a; Palmer et al., 2020). While some studies have suggested neutral biocrust responses to wildfire (Bowker et al., 2004b; Condon et al., 2023), other studies have observed negative outcomes, including losses in microbial community connectivity, moss and lichen cover and biocrust species richness (Haubensak et al., 2009; Root et al., 2017; Aanderud et al., 2019; Palmer et al., 2020). In cases of propagule loss and post-fire soil erosion, biocrust restoration represents a promising nature-based strategy for rehabilitating degraded drylands and enhancing ecosystem resilience (Antoninka et al., 2020b), while also helping to restore multiple ecological functions, including soil stability, hydrology, nutrient cycling and potentially native plant communities (Bowker, 2007; Bowker et al., 2022).

Restoring biocrusts in degraded locations requires the addition of biocrust biota, either obtained from natural biocrusts (preferably prior to a planned disturbance, i.e., salvaged) or cultivated ex situ. Cultivating biocrusts to increase the availability and application of salvaged material is necessary to produce enough inoculum to scale up restoration (Tucker et al., 2020). Greenhouse and field cultivation trials have demonstrated that biocrust can be cultivated and used in restoration (Muñoz-Rojas et al., 2018; Giraldo-Silva et al., 2019; Antoninka et al., 2024). However, translating this production into full functional recovery remains challenging. While cyanobacteria may expand rapidly after inoculation, improvements in soil stability are minimal, and late-successional lichen and moss components typically show limited establishment (Antoninka et al., 2018). The means of field-delivery of inoculum can greatly influence establishment. For example, slurry or broadcast inoculation is easy to apply, but had low establishment, whereas "biocrust sods" provided immediate physical stability and higher survival (Rowe et al., 2026). Biocrust sods are intact, high-biomass biocrust mats produced by cultivating salvaged biocrust on a thin soil layer over biodegradable materials, including weed cloth or burlap (Bailey et al., 2026). This approach allows the biocrust community to develop as a cohesive, physically stable unit that can be rolled, transported and installed directly onto disturbed soils with minimal disruption to community structure (Jech et al., 2025; Rowe et al., 2026). Sods are a promising method to stabilize soil while restoring native biocrust communities in targeted areas, like eroding hillslopes. However, we also need methods that are less intensive for broader distribution of biocrusts and seeds, yet hand or mechanized broadcast of seeds and biocrust inoculum generally have poor success for various reasons (Abella et al., 2009; Doherty et al., 2020; Rowe et al., 2022). Methods that can retain propagules in place, reduce abiotic stress and aid water retention for propagules are needed to improve success. One option is encapsulation and distribution of biocrust biota and seeds in gel capsules that maximize propagule amounts and allow light to penetrate (Mayorga et al., 2026). Capsules are cheap and easy to make and distribute, but have yet to be field tested (Mayorga et al., 2026).

Our study builds on these foundations by testing biocrust sod installations and capsule applications directly in post-fire field conditions. This approach represents an alternative to traditional inoculation techniques (e.g., broadcast of biocrust fragments) and remains relatively unexplored in applied field restoration contexts. By evaluating these methods under real post-wildfire conditions, we aim to assess their potential to accelerate soil stabilization and biocrust and native plant recovery in degraded desert ecosystems. At a burned site draining into Lake Roosevelt in the Tonto National Forest, Arizona, we tested (1) biocrust sods arrayed perpendicularly to erosional features compared to controls and (2) biocrust and seed capsules compared to unencapsulated inoculum and controls. This area, previously impacted by construction, was burned in the 2020 Bush Fire that was fueled by invasive grasses and prolonged drought conditions, exacerbating soil erosion. Specifically, we tested the following hypotheses: (1) Biocrust sod treatments will reduce sediment transport, increase soil stability and enhance biocrust establishment compared to untreated controls. We expected sod-treated soils to improve soil compared to controls, consistent with microscale hydrological benefits observed (Rodriguez-Caballero et al., 2012; Faist et al., 2017). (2) Biocrust sod transplants will facilitate the expansion of biocrust cover beyond sod-treated surfaces into adjacent microsites, resulting in higher biocrust cover in biocrust sod-treated plots compared to controls. (3) Biocrust and seed addition, particularly through capsule application compared to dry broadcast, will promote greater biocrust development and native plant establishment relative to uninoculated control plots.

Methods

Site description

Our research site is located within Tonto National Forest in the Sonoran Desert ecoregion adjacent to Roosevelt Lake, Arizona (33.730361 N, −111.212812 W, Supplementary Figure S1). The site occurs on a gentle slope to a moderate steep alluvial fan remnants, dissected alluvial plains and inset fans (USDA Forest Service, Southwestern Region, 2023). The site was previously affected by decades-old highway construction impacts, then burned in the 2020 Bush Fire, which burned over 193,000 acres in Tonto National Forest, northeast of Phoenix, AZ, USA, making it one of the largest desert-scrub fires in Arizona's history. The burn severity at the site was low (USDA FS, 2020; USGS and USDA FS, 2026). See Supplementary Figure S1 for details regarding soils, biocrusts and plant community at the site. The mean annual precipitation (30-year normals) at the site is 38.1 cm and the mean annual air temperatures range from 12.7 to 28.4 °C (Supplementary Table S1). The first winter season, when sods were installed, had slightly above normal precipitation, but the following summer and winter were substantially below normal (Supplementary Table S1).

Sod experiment – experimental design

In fall 2023, we established ten plots based on visible rill features to directly assess the effectiveness of biocrust sods in stabilizing soils and reducing erosion. To do this, first we identified ten rills and their surrounding runoff producing zones across the site. Using the

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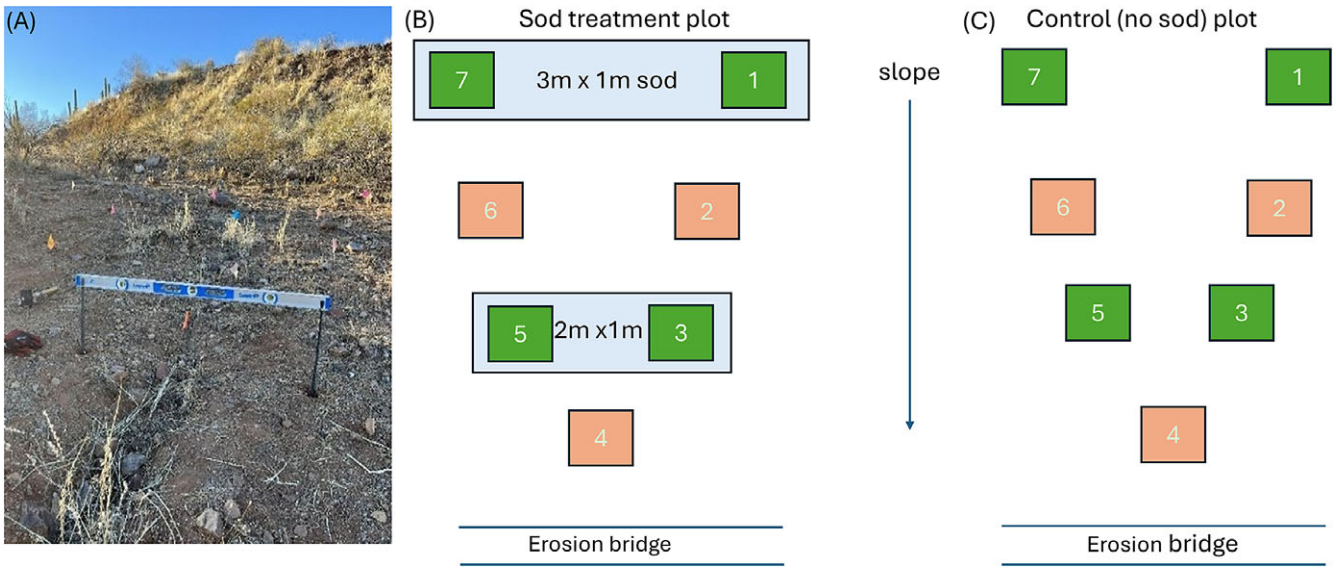


Figure 1. Photo showing (A) erosion bridge installation below plots; (B) schematic diagram of a sod treatment plot and (C) control (no sod) plot showing fixed subplot quadrat sampling positions. Light blue rectangles represent biocrust sods (3 × 1 m and 2 × 1 m). Green squares indicate on-sod subplot positions (1, 3, 5 and 7) and orange markers indicate between-sod positions (2, 4 and 6). Analyses compared either the on-sod positions on the sod treatment plots with the same positions on the control plots or the between-sod positions on sod treatment and control plots. The erosion bridge was positioned 30 cm downslope from quadrat position 4 to measure soil surface changes over time.

ten rills, we paired nearby rills with similar slope, aspect, vegetation and erosion severity resulting in five pairs, 3 m – 13 m apart, located within our 0.5 ha study site. Within each of the five pairs, one rill was randomly assigned as a biocrust sod treatment plot, while the other served as an untreated control (Figure 1). Each pair represented one block to control for local differences in slope and erosion severity in the statistical models.

Biocrust sod cultivation and farm site

We cultivated biocrust sods at Scottsdale Community College (SCC) grounds (33.513788° N, 111.879778° W; Arizona, USA) from November 2022 until December 2023. The average precipitation at this site is 220.15 mm and the temperature averages 22.9 °C with highs reaching over 40 °C in the summer (1991–2020 Normals, PRISM data downloaded 8-11-2025). The temperatures ranged from 0.4 °C to 46.8 °C during the cultivation growing period (PRISM data downloaded 01-30-2026). The site was cleared of debris and leveled for a previous experiment (Antoninka et al., 2024).

Sod cultivation followed the general cultivation framework of Antoninka et al. (2024) but instead of small plots, we grew the sods in long continuous rows, 1 m wide and 18–21 m long on top of a heavy plastic 20-year weed-blocker to exclude exotic invasive plants. In November 2022, we installed sods with a biodegradable weed cloth base (sheets of maize-derived poly-lactic acid, Vigoro), a 0.5 cm layer of substrate (2 L Quikrete graded and washed coarse sand m^{-2}), topped by a continuous sheet of finely woven burlap fabric and finally a layer of salvaged biocrust sieved through 0.4 cm mesh and applied evenly over the burlap to achieve 20.2% biocrust surface cover (0.47 ± 0.86% cyanobacteria, 2.47 ± 0.92% moss and 17.65 ± 7.57% lichen) across the full sod length (200 mL/m^2). We originally salvaged the biocrust prior to the construction of a trailhead in the McDowell Sonoran Preserve (33.7464, −111.8883, < 100 miles from the study site) in October 2019 and stored in the dark at ambient temperatures. Drip irrigation was installed, with a 50% shade cloth laid on the top to retain moisture and prevent overheating. During the initial cultivation period (November 2022–April 4, 2023), the sods were watered four–five times daily in short (2–3 min) cycles, maintaining continual hydration. Weeding was conducted by hand-clipping to avoid disturbing the developing crust. We irrigated the biocrusts during optimal growing temperatures (< 27 °C) and ceased irrigation in summer to allow natural dormancy during these stressful conditions. We re-established irrigation from mid-October to mid December 2023 (8 weeks), resulting in visible increases in total biocrust cover as seen on baseline measurements at time of installation.

Sod harvest and field installation

In mid-December 2023, we weeded, cut sods into 2 m and 3 m long sections and rolled sods around a PVC pipe for transport. For rolling, the biocrust surface was kept inward. Sods were kept moist during handling with plastic covering and transported to the field site within approximately 24 hours of harvest.

At the study site, we unrolled sods onto sod treatment plots, carefully peeling off the biodegradable weed cloth during the process, leaving the burlap layer as the base. We did so to make these sods permeable to vascular plants, thereby assisting with soil surface stability. Each sod treatment plot received two sods: one upslope 3 × 1 m sod and one downslope 2 × 1 m sod positioned 1 m apart, installed perpendicular to the main slope to intercept runoff and stabilize developing rills (Figure 1). Two sods were applied to create redundant interception opportunities for runoff and sediment, while spacing and length of the two sods were based on the dimensions of the plot.

Biocrust and plant sampling

We marked seven fixed sampling subplots (Figure 1B,C) per plot to guide repeatable quadrat placement. The four "on-sod" subplots were each positioned over the sod-covered areas (two per sod piece, 30 cm from edges; Figure 1B), or in equivalent areas where sods

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would have been placed in control plots. Three "between-sod" subplots were established to monitor whether sods facilitated biocrust colonization between sods in both sod treatment and control plots (Figure 1B,C).

To sample biocrust and soil coverage, we used the grid-point intercept method (30 cm by 30 cm quadrat) in the subplot locations in March 2024, October 2024 and March 2025. Soil surface categories included: bare soil, cyanobacteria (light and dark), lichen, moss, jute, litter and rock (<2 mm, 2 mm < 10 cm, 10 cm < 30 cm and > 30 cm). Any biocrust categories not intercepted but present in the plot were recorded as an additional 0.5 point. We calculated the percentage of total biocrust cover by summing cover of lichens, mosses, light cyanobacteria and dark cyanobacteria. Late-successional biocrust cover was calculated as the sum of dark cyanobacteria, lichen and moss cover, omitting early successional light cyanobacteria. We visually estimated total plant cover in Spring 2024.

Erosion and soil stability sampling

At the bottom of each plot, but immediately upslope from a developing gully, we installed an erosion bridge to measure distance to the soil surface (Figure 1A) (Shakesby, 1993) and measured the center 14-pin positions in December 2023, March 2024 and February 2025. To normalize the soil surface elevation changes with baseline for analysis, we calculated the differences for each of the 14 individual pin positions per erosion bridge by subtracting baseline values (December 2023) from the subsequent measurement (March 2024) for the 2023–2024 difference and March 2024 from the February 2025 measurement (2024–2025 difference).

To test our hypothesis that biocrust increases soil stability, we took three complementary field measurements at the beginning (December 2023) and at the end of the experiment (February 2025). We followed established protocols to measure soil stability using the Jornada soil stability test kit (Herrick et al., 2001), soil shear strength, using a Torvane shear device (DGSI-Durham Geo Slope Indicator) (Brunori et al., 1989) and a pocket penetrometer (Forestry suppliers #77114) to measure unconfined compressive strength (Mousavi et al., 2021). In December 2023, one measurement per device was collected at each between-sod subplot, totaling 30 measurements per device. In February 2025, we improved precision by collecting three measurements per device at the same subplots, resulting in 90 measurements per device.

Capsule experiment: experimental design and treatments

In December 2023, we marked three 30 × 30 cm plots (each ≥ 30 cm apart) in each of ten bare areas (blocks) lacking visible biocrust at least 7 m away from sod plots at the same study site (30 plots total). Within each block, treatments were randomly applied to one of the three plots: (1) capsule application, (2) broadcast application or (3) untreated control in a randomized block design.

Capsules were formulated with biocrust organisms and seeds and diatomaceous earth to deter ant herbivory (Korunic et al., 2016). Each treatment plot received: 6.3 g of diatomaceous earth, 90 mL of salvaged biocrust material and 1.24 g of seeds, spread over the plot evenly either in capsule or broadcast form. To assure that the capsule plots had the same materials, we measured out the materials and filled the capsules for each plot separately. We used a manual capsule-making device (CAPSULE-IT, HerbAffair.com). All plots were covered with biodegradable jute netting to retain soil moisture and added biological materials. The salvaged biocrust material had the same origin as that used for sod cultivation, then cultivated in the Northern Arizona University (NAU) greenhouse following methods by Antoninka et al. (2024), generally resulting in biocrust comprised of 40% moss, 20% lichen and 60% cyanobacteria (Antoninka unpublished). The native seed mix applied to each plot included ~200 viable seeds each of three species: three-awn grass (*Aristida purpurea*, 0.37 g per plot), sideoats grama (*Bouteloua curtipendula*, 0.76 g per plot), and desert marigold (*Baileya multiradiata*, 0.11 g per plot). Seed weights were calculated using species-specific purity adjustments provided by the seed provider (CactusStore.com, Phoenix, AZ).

We followed the same methods described above to measure biocrust cover within 30 × 30 cm quadrats placed within each plot at three-time points: March 2024, October 2024 and March 2025. We also counted individuals of the seeded plant species in March 2024.

Statistical analysis

All statistical analyses and data visualization were conducted using R version 4.3.1 (R Core Team, 2021). Analyses were performed using the following packages: *lme4* for linear mixed models (Bates et al., 2015), glmmTMB for zero-inflated, generalized linear mixed models (Brooks et al., 2017), *emmeans* for estimated marginal means and post hoc comparisons (Lenth et al., 2021) and *ggplot2* for data visualization (Wickham, 2009). We used linear regressions to calculate predicted values across the range of observed data values using the function ggpredict() from the package *ggeffects* (Lüdecke, 2018). Where appropriate with a significant main or interaction effect, Tukey's HSD was used for post hoc pairwise comparisons ($\alpha = 0.05$) using *multcomp* (Hothorn et al., 2008).

We applied 16 linear mixed models across the two experiments (see model details in Supplementary Table S2). For seedling counts collected in March 2024, a zero-inflated, generalized linear mixed model with a Poisson distribution and log link function was used to assess the fixed effect of treatment (three levels: capsule, broadcast and control) with block as a random effect. We examined residuals for each model and improved normality of model residuals by applying transformations (Supplementary Table S2).

Results

On-sod biocrust cover

Season, treatment and their interaction were all significant predictors of both total and late-successional biocrust cover for the on-sod treated plots (Figure 2 and Supplementary Table S2). Sod-treated subplots had significantly higher late-successional biocrust cover than control subplots in all sampled seasons, with the strength of the difference varying among seasons (Figure 2A). At the final timepoint of the study (March 2025), mean late-successional biocrust cover in on-sod positions was almost eight times more on sod plots (39.69 ± 1.69%) compared to on control plots (5.20 ± 2.45%; Supplementary Table S2). For the same on-sod positions, total biocrust cover was almost two-times higher on sod plots (41.08 ± 1.66%) compared with control plots (23.20 ± 4.0%; Supplementary Table S3).

Between-sod biocrust cover

We found no significant sod treatment effect or significant interaction between treatment and season (Figure 2B,D and Supplementary Table S3). However, there was a significant season effect (Supplementary Table S3 and Figure 2B,D), in which

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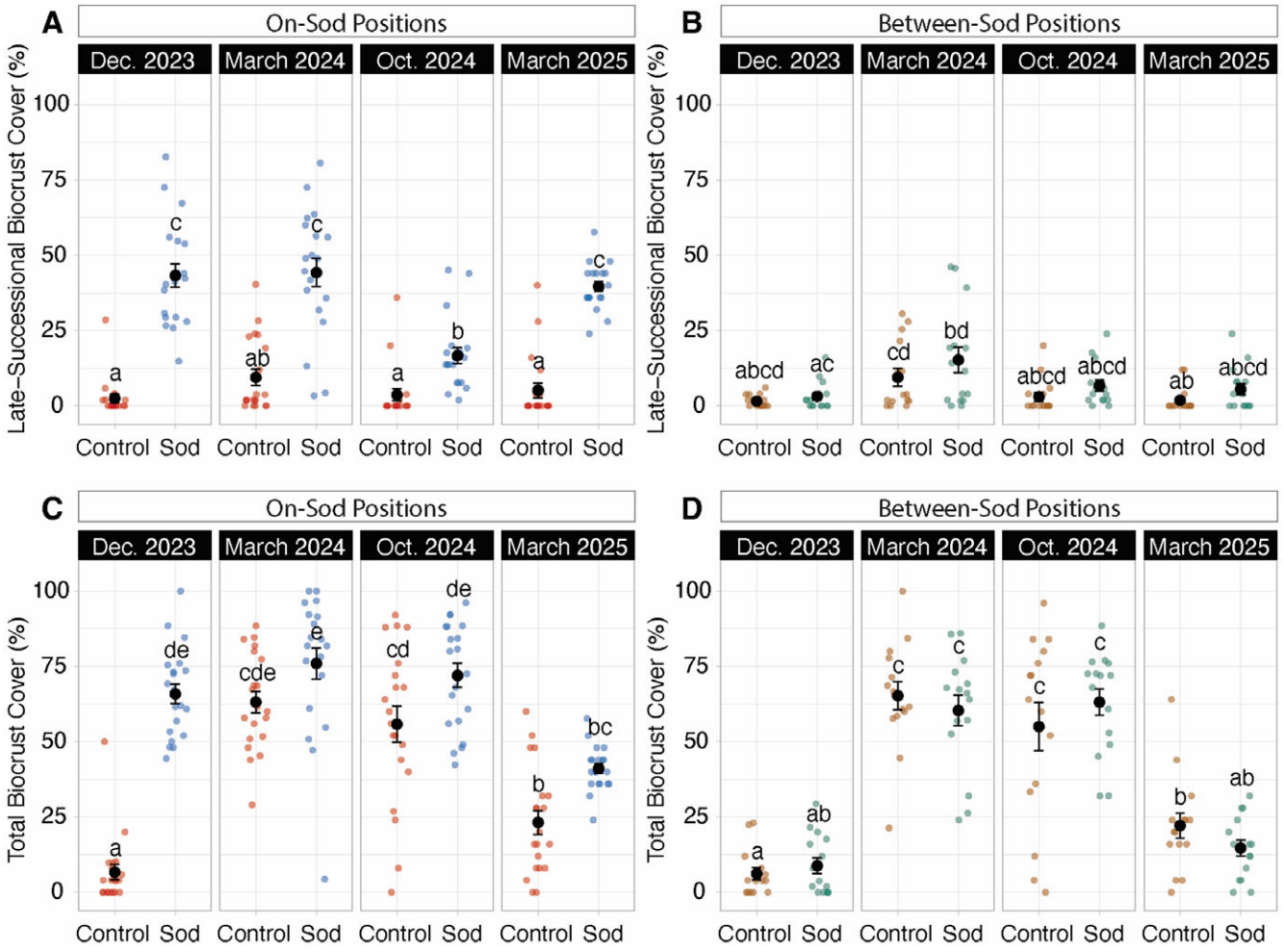


Figure 2. Seasonal and treatment effects on late-successional biocrust in (A) on-sod positions and (B) between-sod positions and total biocrust cover in (C) on-sod positions and (D) between-sod positions. Treated (sod) and control plots were compared within each position. Biocrust cover (%) was measured on four sampling dates: December 2023, March 2024, October 2024 and March 2025. Mean (black dot) and standard error (black bars) are shown for each treatment group; colorful points display the raw data points. Letters indicate differences among treatments based on Tukey's HSD tests.

late-successional biocrust was highest in March 2024 and total biocrust cover was highest in March and October 2024.

Plant and biocrust cover relationships

Sod treatment alone was not a significant predictor of plant cover in spring 2024 for either on-sod ($F_{1,34} = 0.22$, $p = 0.643$) or between-sod ($F_{1,24} = 0.50$, $p = 0.485$) positions in linear mixed models. However, the relationship between plant cover, biocrust cover and treatment was more complex. With plant cover as the response variable, linear mixed model regressions indicated a significant negative slope resulting from the interaction of sod treatments and late-successional biocrust cover in between-sod positions ($F_{1,25} = 4.482$, $p = 0.044$; Figure 3B and Supplementary Table S4), indicating that as late-successional biocrust cover between sod plots increased, plant cover decreased. Total biocrust cover, treatment and the interaction of total biocrust cover and treatment were all marginally significant ($p < 0.1$) predictors of plant cover in between-sod positions (Figure 3D and Supplementary Table S4); however, these marginally significant relationships did not hold when a single outlying point with anomalously high plant cover was removed. There was no statistically significant relationship between plant cover, total biocrust cover, late-successional biocrust cover or treatment for on-sod positions (Figure 3A,C).

Erosion bridge

We detected no differences in distance-to-surface measurements for treatment or the interaction with season, based on erosion bridge data (Supplementary Table S5). However, there was an effect in which in the first year both the treatment and control plots accrued soil, but lost soil in the second year (Supplementary Table S5 and Figure 4A).

Soil stability

Differences in soil stability between sods depended on the season sampled; no differences were detected between control and treated plots at the time of installation, December 2023, but by February 2025, sod plots exhibited significantly higher stability scores than controls ($F_{1,88} = 4.71$, $p = 0.033$, Supplementary Table S5 and Figure 4B).

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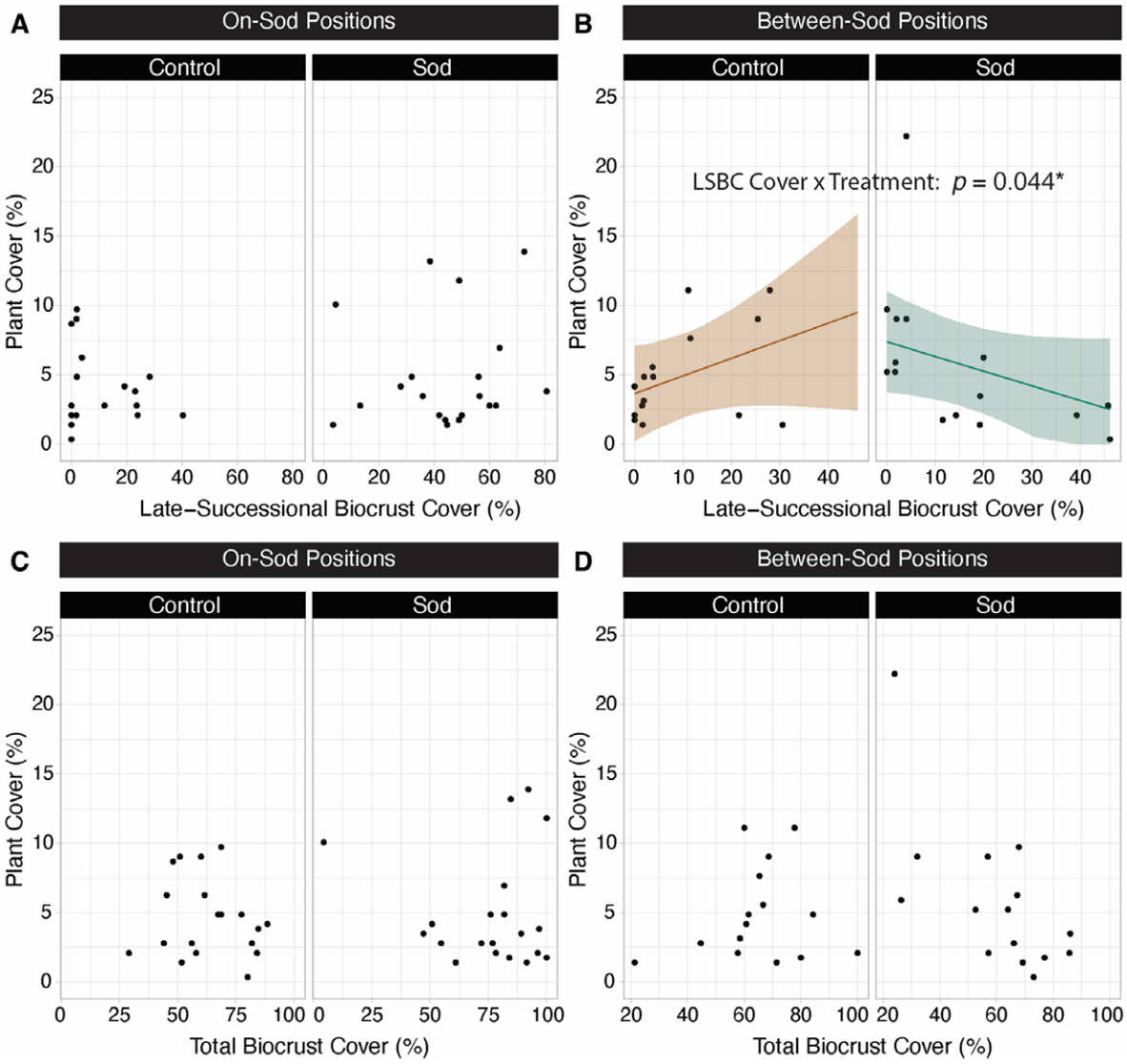


Figure 3. Linear regressions of plant cover (%) in relation to (A) late-successional biocrust cover in on-sod positions, (B) late-successional biocrust cover in between-sod positions, (C) total biocrust cover in on-sod positions and (D) total biocrust cover in between-sod positions. Black dots depict raw plant cover data. Lines show predicted estimates from linear mixed models and colored ribbons show the bootstrapped 95% confidence intervals for predicted values with random effect variance set to zero. Significant predictors ($p < 0.05$) of plant cover as determined from linear mixed models are noted where they exist in panel B; otherwise, the plotted relationships were not statistically significant predictors of plant cover.

Penetrometer and Torvane

We detected no differences in penetrometer resistance across treatments or season (Supplementary Table S5 and Figure 4C). We detected a difference in season, in which shear strength (Torvane) was greater at the end of the study, compared to initial conditions (Supplementary Table S5 and Figure 4D), but we detected no sod treatment differences.

Capsule experiment biocrust and seed application

Treatment and season were both significant predictors of late-successional biocrust cover in the capsule experiment (Supplementary Table S3). Averaged over all three seasons, the capsules resulted in higher late-successional biocrust cover than the no biocrust control plots and marginally higher late-successional biocrust cover ($p = 0.08$) compared with the broadcast treatment (Figure 5A and Supplementary Table S6). By March 2025, late-successional biocrust cover was as follows, mean ± SE: 16 ± 3.73% in capsule plots, 10.4 ± 3.33% in broadcast plots, and 4.8 ± 2.22% in control plots. Averaged across all treatments, late-successional biocrust cover was highest in March 2024 and lowest in March 2025; October 2024 values were intermediate between the two (Supplementary Table S3 and Figure 5A).

Season, but not treatment, had a significant effect on light-cyanobacterial cover (Supplementary Table S3 and Figure 5B). Mean light-cyanobacterial cover did not differ between March 2024 and October 2024, however, values declined significantly by March 2025 (Figure 5B). *B. multiradiata* (desert marigold) seedlings were the only seeded species observed in March 2024. The average number of *B. multiradiata* seedlings per plot differed among treatments such that broadcast (seedling mean ± s.e.: 7.1 ± 1.83) and capsule (6.7 ± 1.09) treatments were not different from each other, but different from the unseeded control (0.0 ± 0.00) plots ($Z = -2.45$, $P = 0.014$).

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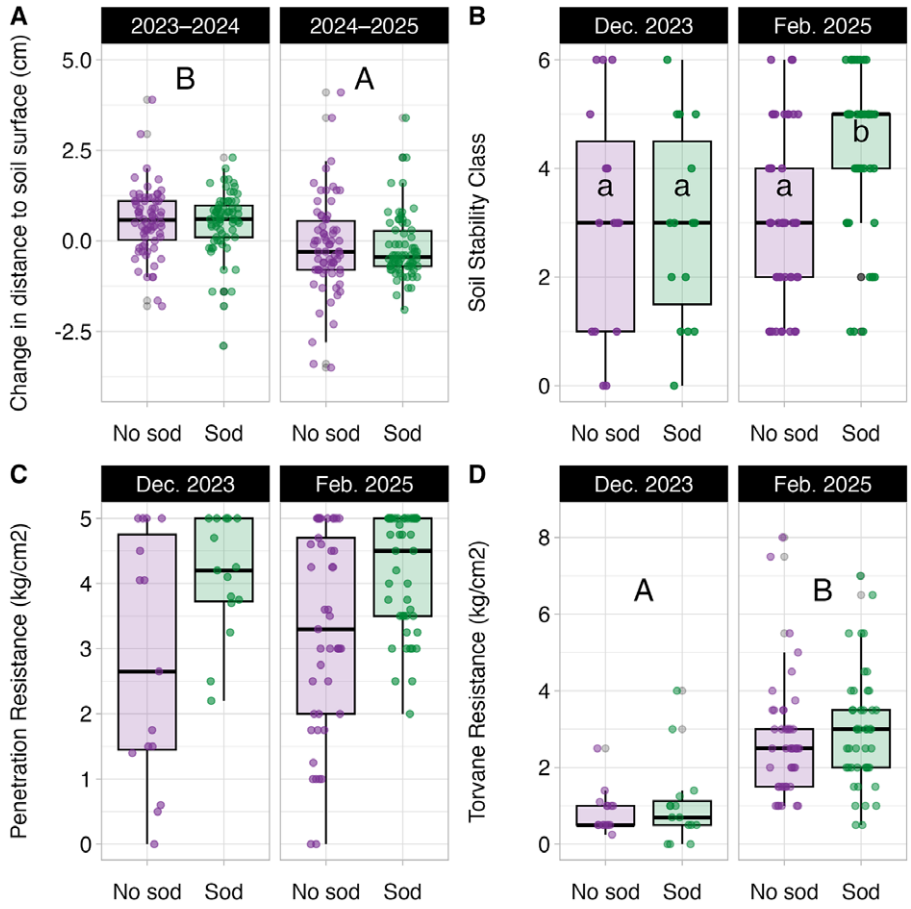


Figure 4. Effects of treatment (sod and no sod) and time on (A) erosion bridge measurements – change in distance to soil surface (cm), (B) soil stability class, (C) penetrometer resistance (kg/cm^2) and (D) Torvane shear resistance (kg/cm^2). Change in distance to soil surface was calculated by subtracting December 2023 erosion bridge measurements from March 2024 (2023–2024) and March 2024 measurements from February 2025 (2024–2025). Negative values indicate erosion, while positive values indicate sediment deposition. Box plots show the median (line), interquartile range (box, 25th – 75th percentile) and outliers (points beyond 1.5× IQR). Lower case letters indicate differences among treatments * time and upper case letters indicate differences among seasonal differences/time based on Tukey's HSD post hoc analysis for significant interactions.

Discussion

By the end of this 2-year study, we found that we were able to successfully accelerate biocrust recovery using two distinct techniques (sods and capsules) in a degraded, burned system. Consistent with hypothesis 1, biocrust sods increased late-successional biocrust establishment and led to enhanced soil aggregate stability between sods. Contrary to hypothesis 1, sod application had no effect on water erosion, soil resistance to penetration or shear strength. Hypothesis 2 was not supported because we detected no visible evidence that sod application colonized outward from the sods. Hypothesis 3 was partially supported in that encapsulated biocrust addition resulted in more biocrust coverage than controls, while broadcast biocrust addition did not. However, native plant seeding resulted in greater establishment of one of the seeded species regardless of encapsulation.

Biocrust sods successfully establish biocrusts, but colonization did not spread

We found that biocrust sods significantly increased both late-successional and total biocrust cover. The sods themselves maintained late-successional cover of ~40% after 2 years, which is comparable to or better than some of the most successful biocrust restoration practices (Condon and Pyke, 2016; Doherty et al., 2020), using either cultivated biocrust inoculum (Wang et al., 2009; Doherty et al., 2020) or field-sourced biocrust inoculum (Condon and Pyke, 2016). Multiple outcomes of biocrust inoculation have been documented: (1) added biocrust inoculum does not speed biocrust development relative to background rates (Young et al., 2019; Faist et al., 2020), (2) a steady progression of growth or successional development is observed (Lan et al., 2014) and (3) biocrusts fluctuate in abundance or development after inoculation (Condon and Pyke, 2016; Doherty et al., 2020). Fluctuations in biocrust abundance during restoration are commonly attributed to weather and climate differences between seasons and years (Doherty et al., 2020; Antoninka et al., 2020a). Here, we observed apparent seasonal fluctuation, most notably as a decline in cover measured after the only summer in our monitoring period, followed by a substantive rebound to the level of cover observed in the previous cool season. Biocrusts are only active when hydrated. In ecosystems that receive cool season precipitation (mid-autumn to mid-spring), it is often observed that periods of biocrust growth or net photosynthetic activity are concentrated in the cool season as opposed to the summer (Darrouzet-Nardi et al., 2015; Han et al., 2022). In contrast, warm season hydration periods can be stressful for some

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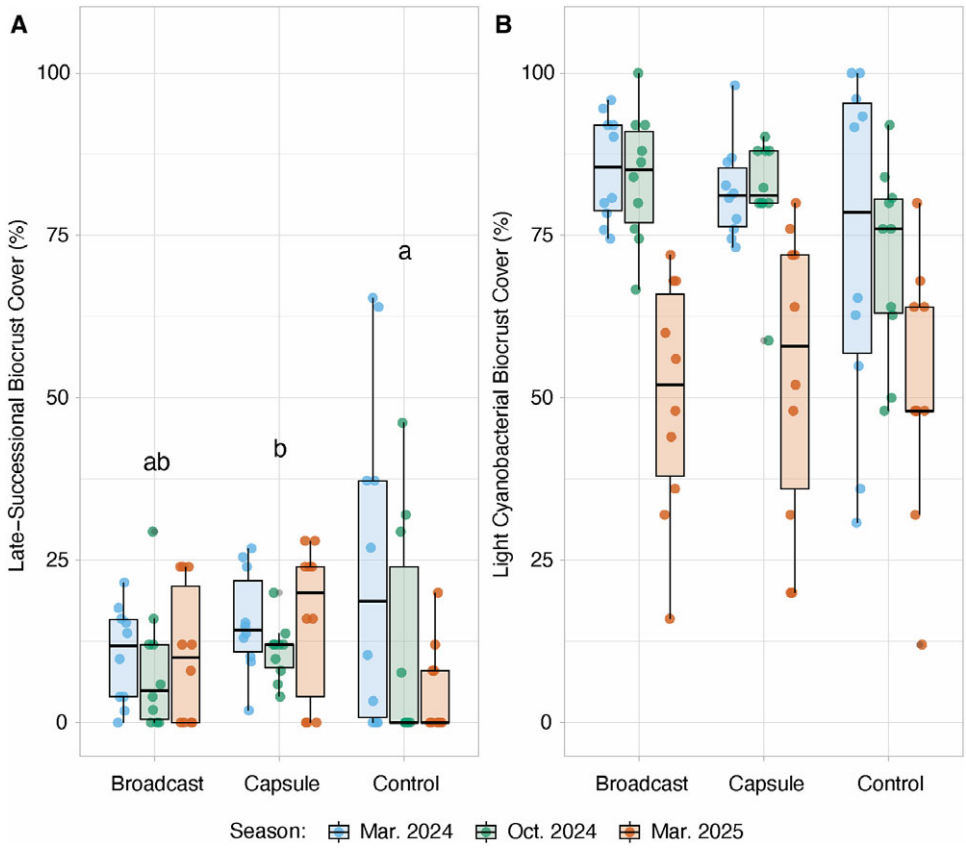


Figure 5. Differences in broadcast, capsule and control treatment effects on (A) late-successional biocrust cover and (B) light cyanobacteria across all three sampling seasons. Boxes show the median (black line) and interquartile ranges (box); colored dots show the raw data points for each season/treatment combination. Lowercase letters indicate differences in treatment effects averaged over season based on Tukey's HSD post hoc analyses of linear mixed models. Season was statistically different for both models. Late-successional biocrust was higher in March 2024 than March 2025, but was not significantly different in October 2024 compared to the other sampling periods. Light cyanobacteria was significantly higher in the first two seasons compared to the final season (March 2025).

biocrust biota because temperatures are supraoptimal and hydration periods too short to allow full recovery from the preceding desiccation event (Coe et al., 2012).

Biocrust sod application promotes soil aggregate stability, but does not affect erosion

Biocrusts are a well-documented soil stabilizer (Huang et al., 2025) and can strongly influence the development of vascular plant communities, which also stabilize soils (Song et al., 2017). Thus, a major motivating factor in our research was to determine if biocrust sods could be used to stabilize soils and reduce erosion in a site degraded by multiple disturbances, including fire. Sod treatments provided measurable improvements in soil stability of soil surfaces in between sod placements, in the second year. The sods themselves consist of well-aggregated, fabric-reinforced soil that confer immediate reductions in erodible soil surface, and these results indicate that sod use can continue to improve plot-scale soil aggregate stability over time in surfaces near to but not covered by sods. Though our visible cover data did not clearly demonstrate biocrust colonization or an increase of plant cover, we suggest that sods could have physically reduced movement of sediment into and out of the interspaces among sods, protecting soil intactness of soil aggregates, and increased the propagule supply of biocrust biota, boosting cryptic incipient biocrust formation and creation of new aggregates. These two effects cannot be clearly separated given our data, and either or their combination could have induced the patterns we observed.

Soil shear strength was temporally dynamic, increasing ~3-fold from the beginning of our experiment until the second observation. This finding aligns with the observed temporal increase in soil aggregate stability, suggesting an overall trend of increasing erosion resistance. However, unlike soil aggregate stability, these data did not support an influence of sod placement. Soils with greater soil aggregate stability would generally be expected to also have greater shear strength, but the measurements are based on distinct principles and do not always align (Mallen-Cooper et al., 2020). Penetrometer measurements neither increased through time nor with sod placement. While penetration resistance can be a negative indicator of soil surface wind erosion resistance (Li et al., 2010), it may also reflect compaction, density or lower porosity (Mallen-Cooper et al., 2020). Possibly these properties were static during our experiment or the site experienced counter-balancing change in more than one of them.

The effects of sod treatment on soil aggregate stability did not translate into measurable differences in erosion, as measured by the erosion bridges. Erosion bridge data showed that treatments had nearly identical changes in surface elevation: in the first year we detected a loss of surface height (indicating net erosion), but in the second year we detected a nearly equal gain of surface height

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(indicating net sedimentation). This temporal effect may be linked to increasing soil aggregate stability and shear strength through time or it may be linked to differences in rainfall. The low rainfall in the second year was possibly only sufficient to transport sediment from our plots a short distance, resulting in sedimentation where the erosion bridges were located.

Capsules promote biocrust establishment, but neither help nor hinder seeding success

In the capsule experiment, late-successional biocrust cover showed statistically significant differences across treatments, with capsule applications producing significantly higher cover than control, whereas broadcast biocrust additions did not produce higher cover than controls. These results suggest that capsules may increase the probability of a successful inoculation within 2 years and can establish the presence of taxa typically associated with well-established biocrusts. Similarly, Román et al. (2020) demonstrated that cyanobacteria can be successfully incorporated into extruded soil pellets and redistributed across degraded substrates, supporting their viability and effects on early soil surface properties. This effect was somewhat surprising because capsules only persisted for a short period of time due to heavy rain shortly after application which dissolved the capsules. Without these heavy rains, we would have expected a residence time of weeks to months based on previous controlled trials (Mayorga et al., 2026). The short residence time means that the enhanced outcomes were not due to prolonged protection but may instead reflect some combination of the following hypothetical mechanisms: (1) A positive outcome of localized concentration of viable propagules engaging in facilitative interactions, (2) a purely retentive benefit in which the short presence of the capsule helped inoculum fragments bond to each other upon hydration forming larger masses, or in which the soluble, sticky capsule constituents themselves helped adhere the inoculum to the soil (Bailey et al., 2026) or (3) a short-duration amelioration of stress, such as a prolonged hydration event under enhanced physiological conditions (Coe et al., 2012). We cannot discern among these hypothetical explanations with our data but advance them to inform future studies. In addition to biocrust responses, both capsule and broadcast treatments supported robust *Baileya radiata* emergence, a species that did not emerge in control plots. This finding means that although encapsulation did not improve emergence, seed could be successfully co-distributed with biocrust in capsules, promoting both native plants and biocrusts.

Comparing and contrasting emerging biocrust restoration techniques

We tested two very different methods to improve biocrust establishment in this study: biocrust capsules and sods. Though there was a large difference in their effect on treated areas in terms of biocrust coverage and development, their efficacy should not be compared directly because of the different levels of resource and effort input and, accordingly, different application targets. Sods require intensive input to create and are very effective at rapidly inducing a high degree of biocrust development in small, targeted application zones of several square meters over a shorter time horizon. Capsules are relatively quick to make and meant to be more broadly dispersible to ensure the potential for biocrust initial colonization exists across larger areas.

Despite the differences, biocrust sods and capsules are based on a common principle of inoculation coupled with simultaneous retention and habitat amelioration mechanisms (Bailey et al., 2026). We believe that sods are successful because they simultaneously inoculate biocrust propagules, retain them on site by allowing them to attach to fabric-reinforced soil before use and by stabilizing a sufficiently large patch of soil surface, thereby ameliorate the environment. Likewise, capsules not only contain biocrust inoculum but they also promote retention of the inoculum on site, either through greater mass concentration, adherence to soil surfaces or deterrence of animal pests (Mayorga et al., 2026). Both biocrust sods and capsules are newly emergent, thus development of new variants and determination of their efficacy and range of use cases is an ongoing research subject (Bailey et al., 2026). Rader et al. (2022) found that applying a diverse suite of treatments as a bet-hedging strategy in dynamic restoration environments can help buffer restoration projects from uncertainty and potential failure (Rader et al., 2022). Perhaps strategic combinations of these distinct biocrust restoration approaches with each other and with other dryland restoration techniques, such as seeding, will enable more consistent restoration successes in response to a variety of disturbances including wildfire.

Supplementary material. The supplementary material for this article can be found at http://doi.org/10.1017/dry.2026.10054.

Acknowledgments. We are grateful to Scottsdale Community College for providing facilities for the experiment and the McDowell Sonoran Conservancy for providing experimental materials. John Weser, Natalie Case, Nelly Nelson, Seth Charlie, Ryan Yazzie, Michael Sloan, Lydia Bailey, Madeline Mayorga, Jane Brady, Debbie Langenfeld and Mary Fastiggi all assisted in our farm or field site.

AI statement. We used claude.ai (https://claude.ai/new) to shorten and reformat our abstract to the journal's specifications; the revision was then edited by the authors.

Author contributions. All authors contributed to writing; D.O., K.G. and H.I.R. conducted data analyses, and designed figures; M.B., A.A. and H.I.R. conceptualized the experiment; D.O. managed the project and led data collection; all authors contributed to the field work, revised and approved the final version of the manuscript.

Data availability statement. Data and analysis files will be available on https://github.com/ksgriff/Biocrust-Sod-Erosion-Control upon publication.

Declaration of interests. The authors have no conflicts of interest to report.

Funding statement. This work was funded by the Salt River Project (SRP). Elvy Barton served as our SRP advisor.

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https://doi.org/10.1017/dry.2026.10054 Published online by Cambridge University Press