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RESEARCH ARTICLE

Plant effects on biocrusts remained consistent across a gradient of soil stability

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Abstract

Aims Biocrusts are common in arid ecosystems and perform critical ecosystem services. However, how abiotic (soil stability and aspect) and biotic factors (plant species canopies) interact to influence their community composition remains unclear. This study explores whether different plant species host distinct biocrust communities beneath their canopies, and whether these effects vary with slope aspect and soil stability across gypsum dunes. We hypothesized that (i) early-successional cyanobacteria biocrusts dominate unstable soils, while (ii) shade- and moisture-sensitive types prevail on north-facing slopes; that (iii) moss crusts are more frequent under denser canopies; and that (iv) plant-driven microenvironmental effects are stronger in stable soils but converge across plant species in unstable soils.

Methods In White Sands National Park (New Mexico, USA) we assess changes in biocrust community across slope aspect and a soil stability gradient measuring the relative abundance of biocrust types along 27 transects (270 quadrats, 25 cm^2 each). We used linear mixed models and multivariate analyses to compare the changes in relative abundance and composition of different biocrust types amongst these factors and their interactions.

Results Plant species significantly influenced biocrust composition. *Ephedra trifurca* supported more chlorolichen, moss, and cyanolichen crusts, *Tiquilia hispidissima* more incipient crusts, and *Nerisyrena linearifolia* light and dark cyanobacteria. Light cyanobacteria dominated unstable soils; mosses increased on north-facing slopes and under large canopies, while dark cyanobacteria prevailed in open spaces, reflecting their UV tolerance. Unexpectedly, plant effects persisted across soil stability gradient.

Conclusions Our findings advance predictive understanding of biocrust dynamics.

Keywords Biocrust community · Plant–microbe interactions · Plant species effects · Sand dune ecosystems · Restoration · Gypsum

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Introduction

Biocrusts form an integral part of the biotic community in arid and semiarid drylands (Belnap 2003), where limited water availability and high potential evaporation constrain vascular plant growth in arid and semi-arid ecosystems (Noy-Meier, 1973). Biocrusts are special kinds of soil surface aggregates containing communities including photoautotrophic (i.e., cyanobacteria, algae, lichens, bryophytes) and heterotrophic (i.e., bacteria, fungi, archaea) organisms living within the upper millimeters of soil and bind to soil particles in the surface (Belnap et al. 2016; Weber et al. 2022). Biocrust are considered ecosystem engineers (Jones et al. 1997; Oliveira et al. 2022; Xiao et al. 2022) that influence nutrient flow and soil fertility (Elbert et al. 2012; Jassey et al. 2022; Barger et al. 2016; Baumann et al. 2018), impact hydrological cycling (Chamizo et al. 2016a; Chamizo et al. 2016b; Rodríguez-Caballero et al. 2022; Li et al. 2021; Eldridge et al. 2020) or stabilize soils against erosion (Chaudhary et al. 2009; Bowker et al. 2008; Gao et al. 2017). The extent of these services depends on biocrust type, whose distribution is shaped by environmental factors (Pietrasiak et al. 2013). Understanding the drivers of biocrust community structure is therefore critical for predicting their dynamics and for maintaining their ecological functions under global change.

Biocrusts communities can be classified into distinct community types based on their dominant photoautotroph (Pietrasiak et al. 2013). Distinct biocrust types—cyanobacterial, lichen, and moss crusts—can follow a successional trajectory, with early-stage light cyanobacteria giving way to structurally complex dark cyanobacteria, lichens, and mosses (Belnap et al. 2001; Pietrasiak et al. 2013). Cyanobacteria biocrusts contribute to atmospheric N_2 fixation (Barger et al. 2016; Zhao et al. 2010; Nash 2008) but exhibit lower photosynthetic rates than lichens, and mosses (Hoellrich et al. 2023), meanwhile mosses reduce water loss through transpiration (Frey and Kurschner, 1991), improving surface soil water retention (Xiao et al. 2016; Lange 2001) and moderating surface soil temperatures (Xiao et al. 2016). Therefore, biocrust create favorable microenvironments for vascular plants (Ferrenberg et al. 2018; Belnap et al. 2001; DeFalco et al. 2001; Harper and Belnap 2001; Cortina et al. 2010; Li et al. 2000), including plant seedling establishment (Belnap 1995; Xiao and Veste 2017), although how these canopy-driven microenvironments affect biocrust development and composition remains largely unexplored.

Although biocrust organisms can compete with plants for resources such as light, space, and nutrients (Belnap 2003), plants can also facilitate biocrust development, particularly under increasing aridity (Concostrina-Zubiri et al. 2013; Zhang et al. 2016). Plants can shape microenvironments beneath their canopies by generating 'islands of fertility' (Schlesinger et al., 1990) —enhancing nutrient content, retaining soil moisture, and providing UV protection—creating conditions that favor biocrust growth (Bowker et al. 2005; Aguilar and Sala 1999; Kidron 2009; Zhang et al. 2016). These effects can vary among plant species due to their differences in canopy structure, litter deposition, shade or root-mediated water redistribution (Yao et al. 2019; Bochet et al. 2000; Espeleta et al. 2004; Hultine et al. 2003). Understanding the extent to which these plant species-specific effects can shape biocrust composition, and whether they are stronger than abiotic factors, such as moisture, shade, slope aspect or soil stability, could reveal key mechanisms driving biocrust and ecosystem functioning in drylands.

Differences in abiotic biocrust requirements can also drive spatial heterogeneity in community composition. Biocrust-forming mosses are sensitive to rainfall variability (Reed et al. 2012), while cyanobacteria rely less on light protection, as they can produce sunscreen pigments to withstand intense radiation (Castenholz and Garcia-Pichel 2012). Soil properties, such as type and texture (Pietrasiak et al. 2011; Bowker and Belnap 2008; Concostrina-Zubiri et al. 2013), together with slope aspect (Zhou et al. 2020; Chamizo et al. 2016b; Rodriguez-Caballero et al., 2019; Pintado et al. 2005), are key drivers shaping the distribution of biocrusts from local to broader scales (Bowker et al., 2006; Pietrasiak et al., 2013; Rodriguez-Caballero et al., 2019). Although some studies have explored the combined effects of abiotic and biotic factors on the biocrust cover (Ding and Eldridge 2020), plants' influences have been usually assessed for single species and at small spatial scales (Concostrina-Zubiri et al. 2013; Maestre et al. 2008, 2002; Martínez-Sánchez et al. 1994), limiting an integrated understanding of how plant species interact

with abiotic drivers, such as slope aspect and soil stability, to shape biocrust community structure.

In this study we disentangle to which extent biotic factors (i.e. presence of different plant species), abiotic factors (topography, and soil stability) and their interaction drive changes in biocrust community structure along a soil stability gradient of gypsum sand dunes in White Sands National Park, New Mexico. We first tested whether soil stability and slope aspect influence biocrust composition, and then examined whether plant species exert a significant effect, and whether such effects persist across stability levels (interaction between biotic and abiotic factors). Specifically, we hypothesize that (i) early-successional biocrusts (incipient and light cyanobacteria) would dominate low-stability soils, while north-facing slopes would favor insolation-sensitive types such as mosses; (ii) moisture- and temperature-sensitive types of biocrust would be more abundant beneath large-canopy species; and (iii) plant effects on biocrust composition would strengthen with increasing soil stability but converge across species in unstable soils. Accordingly, we expect cyanobacteria to dominate the youngest least stable dune stages, mosses and chlorolichens to be more prevalent on north-facing slopes, dark cyanobacteria and cyanolichens on south-facing slopes, and mosses to predominate beneath species with greater canopy cover. Finally, we expect the influence of plant species on biocrusts to become stronger in more stable dunes, with different plant species harboring distinct biocrust communities under their canopy. In contrast, in early-stage dunes, these differences among plant species may diminish as abiotic factors exert stronger control in the low stability dune stage. Disentangling the roles of vegetation, topography, and soil stability, will advance predictive understanding of biocrust dynamics and highlight pathways for sustaining their ecological functions under global change.

Materials and Methods

Study Area

Data for this study were collected at a gypsum dune field within White Sands National Park, located in the Tularosa Basin in southern New Mexico, U.S.A. White Sands National Park is the largest (~500 km^2) known gypsum dune field in the world (McKee and Moiola 1975; Talmadge 1933). Average annual temperatures in this area range from a high of 24° C to a low of 8° C with a mean annual rainfall of 335.8 mm, with the majority of rainfall (>50%) concentrated between July and October (www.usclimatedata.com).

Experimental design

Data collection was carried out in September–October 2022 along the south-eastern edge of the dune field which is composed of parabolic dunes of different ages indicated by the varying degrees of sediment mobility, vegetation cover, and composition (Fig. 1A). Along this edge of the dune field, we worked at three different sites along a landscape gradient of geomorphic age as characterized by increasing soil stability from gynomorphically young to more mature stabile dunes. The least stable dune stage (youngest gynomorphically) was our north-easternmost sampling area and is closer to the transition zone from more mobile barchan dunes to parabolic dunes, which are more stabilized due to the presence of vegetation (Tsoar and Blumberg 2002). Moving south-west from this point along the dune edge, the parabolic dune substrate increases in stability and transitions from higher vegetation cover and loosely consolidated younger soils to more stable mature soils and reduced vegetation cover.

Field Survey

General characterization of the biocrust community across sites

To assess how biocrust community structure changes across sites, we measured the relative abundance of biocrust types along 27 transects of 25 m each (10 quadrats per transect = 270 quadrats total), distributed across three sites along a soil stability gradient. At each site, we established three transects per slope aspect (north-facing, south-facing and ridge), for a total of nine transects per site. Along every transect, we placed ten 25 cm^2 quadrats at 2.5-m intervals, alternating sides and positioned within one meter of the transect line. Quadrats were always located on bare soil (without

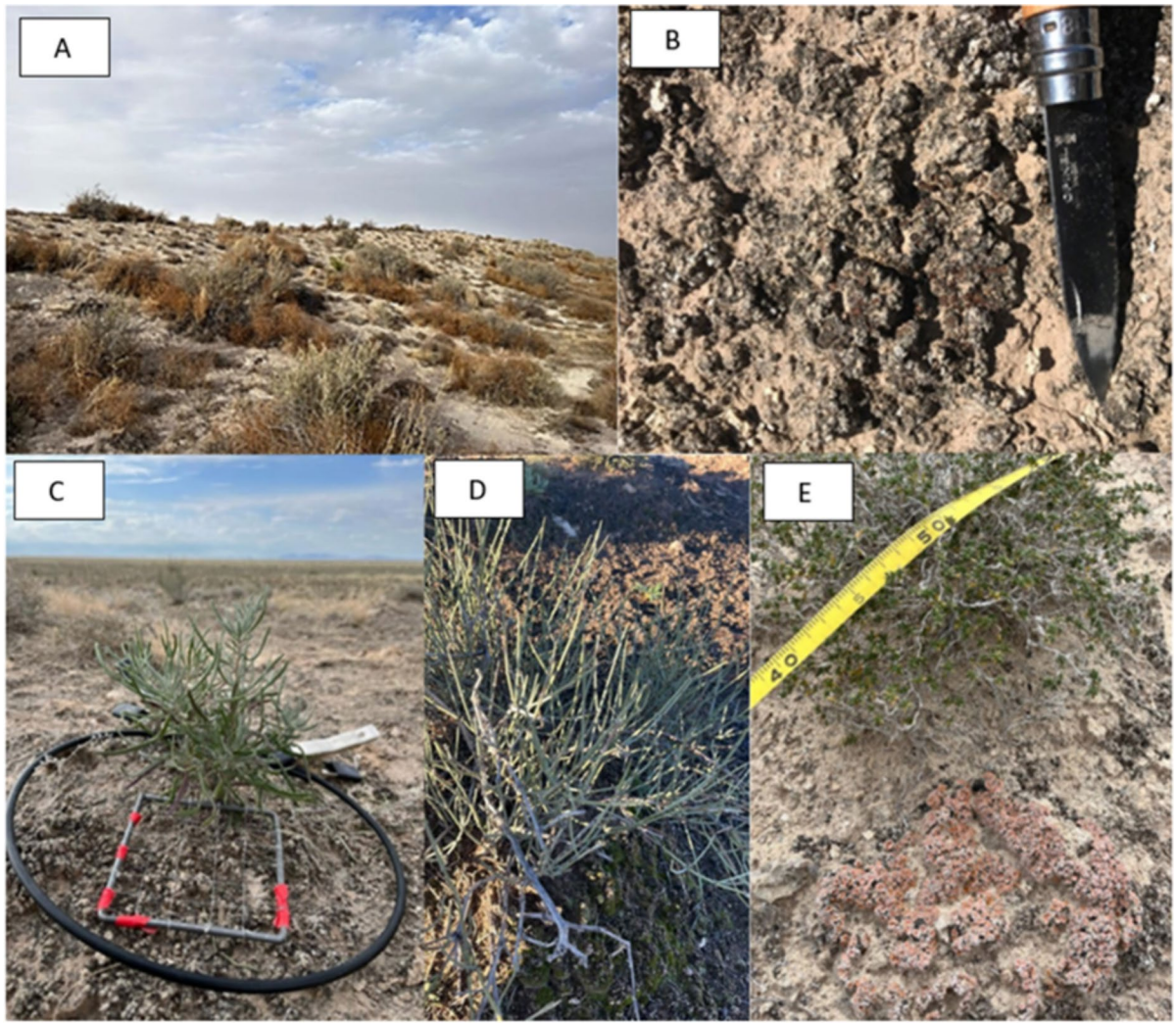


Fig. 1 General view of field work site along the edge of the gypsum dune, which ranged in substrate stability (**A**); chlorolichen-dominated crust (Clavascidium spp.) (**B**); frequency quadrat to identify biocrust beneath the canopy of Nerisyrenia linearifolia (**C**); example of moss-dominated crust beneath the canopy of Ephedra trifurca (**D**); Tiquilia hispidissima along the transect nearby chlorolichen-dominated crust (Psora spp.)

vascular vegetation) to reduce variability associated with microtopography around plants. Each quadrat was subdivided into a 5 × 5 grid (25 intersections). At each point, we recorded the biocrust type present: incipient, light cyanobacteria, dark cyanobacteria, moss, cyanolichen (Collema and Peltula spp.), or chlorolichen (Clavascidium, Psora, Placidium, Fulgensia spp.) (Fig. 1B–E).

General characterization of the plant community across sites

To assess how plant cover, structure, and composition changes across the landscape gradient, we used the same transects described above to assess plant cover. Along each transect, each time a plant touched the transect line, we recorded the plant species, canopy

size, height, and the distance the plant occupied along the transect, which we used to calculate the relative abundance of different plant types (annual/perennial grass, perennial shrub, evergreen shrub, annual/perennial herb) along the landscape gradient.

General characterization of topographic features across sites

To quantify soil stability across the dune edge, we took direct in situ measurements of soil shear strength and soil penetration resistance. Along each of the 27 transects described previously, we used a torsional vane shear test (torvane test hereafter) to measure soil shear strength and a pocket penetrometer to measure soil compression resistance. These measurements were taken on the eastern side of the 25 cm^2 frequency quadrat (no further than 10 cm from it) such that each transect had a total of 10 measurements for both soil test types.

Soil shear strength is a measure of how resistant a soil surface is to frictional forces created by wind and water (Zhang et al. 2018; Torri et al. 2013). To measure soil shear strength, a four-bladed vane is pressed into the soil surface and rotated at a constant rate until the soil surface breaks. The indicator needle on the vane retains the maximum reading, and the values are read directly from the dial (from 0–1 kg/cm^2 in 0.05 kg/cm^2 divisions), and express the torque required to cause a cylindrical surface to be sheared by the vane.

Soil penetration resistance, which is affected by both soil bulk density and soil moisture content, is expressed as the amount of vertical pressure necessary to impact a soil surface (Li et al. 2010). To measure soil compression resistance, we used a metal pocket penetrometer, which is a spring-operated metal shaft that measures compressive strength by pushing a 6.4 mm diameter loading piston into the soil up to a calibration groove in the piston located 0.25 cm from the end of the shaft. Resistance is measured in kg/cm^2 (up to a maximum reading of 4.5), which is indicated by the position of a mobile ring.

Comparison of biocrust beneath plants versus interspace

To compare the influence of plant species identity on biocrust community composition at different sites along a dune stability gradient, we selected three candidate plant species growing in all three sites: *Ephedra trifurca, Tiquilia hispidissima*, and *Nerisyrena linearifolia* (Fig. 1C-E). The genus *Ephedra* consists mainly of perennial evergreen shrubs (around 50 species), which are characterized by needle-like leaves. The distribution of *Ephedra trifurca* is widespread and can be found on both gypsum and non-gypsum substrates (i.e., gypsovag) (Whitford and Steinberger 2020). *Ephedra trifurca* is one of the larger species of its genus and can grow to reach 1 m in diameter and up to 2 m in height and have deep taproots. The arid-adapted genus *Tiquilia* includes around 30 species of annual to perennial prostrate herbs and subshrubs that occur in the deserts of North America and South America. *Tiquilia hispidissima* is a widespread gypsophile species (Moore and Jansen 2007) and is characterized by a wide and low spreading canopy, forming mats 20–40 cm in diameter composed of bristly herbage. The small genus of perennial mustards, *Nerisyrena*, is mostly limited to the Chihuahuan Desert, and most of its species are gypsophiles, meaning they live exclusively on gypsum substrates (Bacon 1978; Meyer 1986). *Nerisyrena linearifolia* is relatively small (it grows to 5–40 cm tall) with long narrow leaves that alternately grow along the stems.

To assess the influence of plant species on biocrust cover, we selected five individuals per candidate species on three aspects (ridge, north, and south) at each of the three dune age stages. Given that plant species and biocrust types could select similar microhabitats based on abiotic factors, we control for this spatial heterogeneity by using a paired design in which each individual plant is paired with an adjacent interspace area (no more than 50 cm from the edge of the plant canopy). To characterize the biocrust living under the influence of the plant, we placed a flexible hose around the circumference of the plant and within this area we placed a 10 cm^2 frequency quadrat frame comprised of 20 intersection points around the base of the plant in the four cardinal directions and record what was observed on the soil surface at each of the intersections (5 individuals × 20 points × 4 cardinal directions = 400 points per plant species per dune stage and aspect). The hose was then placed in the paired (adjacent) interspace to control for observing biocrust within the same fixed area and we measured the frequency of biocrust types in the quadrat and then looked for any unrecorded species, as we did in

the area around the plant. For each plant and interspace pair, the same area was observed around the plant and in the interspace of the plant, but it could be manipulated between pairs to adjust for differences in the size of the plant canopy between individuals.

Statistical Analyses

Analyses were conducted in three steps: (i) sites characterization (i.e. dune soil stability, biocrust and plant cover, structure, and diversity), (ii) effects of abiotic ((i.e. soil stability, slope aspect) and biotic (plant species) factors on the distribution and community composition of biocrusts, and (iii) interaction effect between soil stability and plant species. All analyses were performed in R v.1.4.1717 using GLMMTMB (Brooks et al., 2017) for generalized linear mixed models (GLMMs), emmeans for post-hoc tests (Lenth et al., 2018), and vegan for community analyses (Oksanen et al., 2022).

General site characterization

Soil stability (penetration resistance and shear strength) was compared among geomorphic dune age stages (dune stage hereafter) with two separate GLMMs, where dune stage was a fixed effect and transect nested within slope aspect × dune stage was a random effect; response variables were log-transformed.

Biocrust vs. non-biocrust cover was analyzed with a GLMM including the same fixed and random effects. To explore differences in plant cover across dune stages and aspects we fitted a generalized linear mixed model with dune stage as a fixed effect and slope aspect nested in dune stage as a random effect. Plant cover was calculated as the total distance occupied by vegetation along a transect divided by the length of the transect (25 m).

Differences in biocrust and plant community composition across the soil stability gradient (i.e. among dune stages) were tested with PERMANOVAs (Anderson, 2001) based on relative abundances. Differences in diversity across dune stages were assessed with two separate generalized linear models for biocrust and plant community using the Shannon Diversity Index 'H' for the plant and biocrust community respectively as the response variable. The model for plant community diversity had dune stage as a fixed effect and the interaction between dune stage and aspect as random effect. For biocrusts, the same model structure was used with transect nested within dune stage × aspect as an additional random effect.

Influence of abiotic and biotic factors on biocrust

The influence of soil stability, slope aspect, plant species identity, and their interactions on biocrust composition was tested with PERMANOVAs. Significant effects were further explored with canonical discriminant analysis (CDA) to visualize how the biocrust community structure differs between groups (i.e., dune age stage, aspect or plant species) and identify the linear combination of variables that maximizes the community differences.

Quantifying the effect of plant species on biocrust

To assess the magnitude of the effect of different plant species on biocrust community composition, we fitted separate generalized linear mixed models for each biocrust type (i.e., incipient, dark cyanobacteria, light cyanobacteria, moss, cyanolichen, and chlorolichen). We fitted separate GLMMs using the difference in relative abundance of each biocrust type beneath canopies vs. paired interspaces as the response. In all models, plant species was a fixed effect, and dune stage × slope aspect a random effect. Differences among plant species were tested with Tukey post-hoc comparisons.

Results

Characterization of the sites

Soil stability

The shear vane measurements differed significantly between the three dune age stages ($X^2_{2,\ 270} = 15.2$, $p < 0.001$). It was required significantly more force (kg/cm^2) to break the upper layer of soil in the high stability dune stage (i.e. fixed dune) (estimated

mean ± SE, 1.3 ± 0.07) compared to the low stability dune (i.e. moving dune) (0.96 ± 0.07, $p < 0.001$). The shear vane strength of the soil in the medium stability dune stage (i.e. semifixed dune) was marginally significantly lower than the fixed dune (1.1 ± 0.07, $p = 0.06$) and did not differ significantly from the moving dune ($p = 0.27$; Fig. 2(A)). Soil penetration resistance differed significantly among dune stages ($X^2_{2, 270} = 19.6$, $p < 0.001$). A significantly greater amount of vertical pressure (kg/cm^2) was required to penetrate the soil surface in both the semifixed (1.3 ± 0.05, $p = 0.001$) and fixed (1.2 ± 0.05, $p = 0.002$) dune stages compared to the moving dune (0.98 ± 0.05). The semifixed and fixed dunes did not differ significantly in soil penetration resistance ($p = 0.76$; Fig. 2(B)).

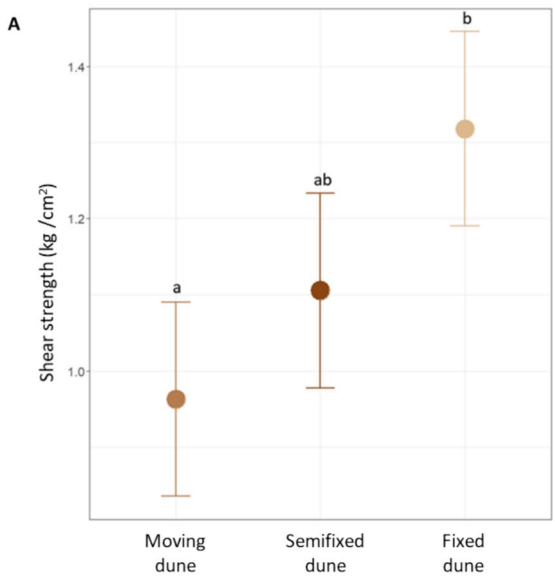
Biocrust community

Biocrust cover (%) significantly differed across the three dune stages ($X^2_{2, 270} = 18.9$, $p < 0.001$). There was a significantly higher presence of non-biocrust cover in the semifixed (2.3 ± 0.4, $p = 0.02$) and fixed (2.7 ± 0.4, $p < 0.001$) dune stages compared to the moving dunes (0.32 ± 0.4). Differences between the semifixed and fixed dunes were not significant ($p = 0.71$).

The relative abundance of different types of biocrust (Fig. 3A; Table S1) differed significantly between dune stages (PERMANOVA, $R^2 = 0.48$ $p < 0.001$). The diversity of the biocrust-types (Shannon Diversity 'H') differed significantly across dune stages ($X^2_{2, 270} = 57.0$, $p < 0.001$) with greater biocrust-types diversity in the semifixed (1.3 ± 0.05, $p < 0.0001$) and fixed (1.2 ± 0.05, $p < 0.0001$) dunes compared to the moving dunes (0.785 ± 0.05). The diversity of the biocrust-types in the semifixed and fixed dunes did not significantly differ ($p = 0.89$).

Plant community

In the moving dunes, there was significantly higher plant cover (33.2 ± 24.1%) compared to the sites with semifixed and fixed dune stages (10.1 ± 4.3% and 9.3 ± 5.0%, respectively) ($F_{2,24} = 16.10$, $p < 0.001$). There was a significant interaction effect between dune stage and aspect ($F_{4, 24} = 5.0$, $p = 0.01$). In the semifixed and fixed dunes, plant



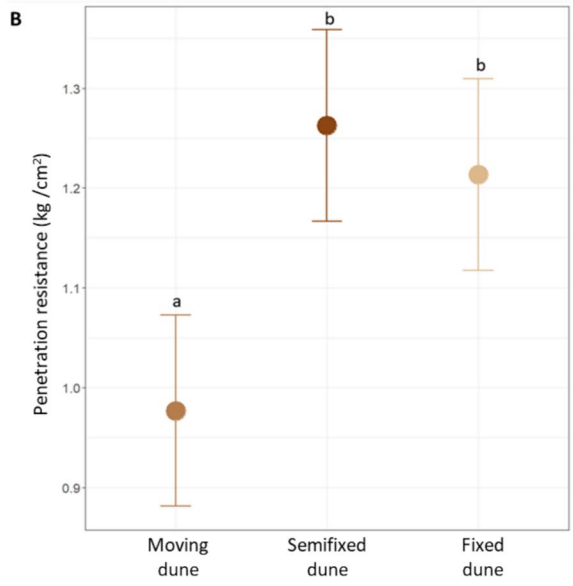


Fig. 2 Estimated marginal means ± 95% CI of (**a**) soil penetration resistance and (**b**) soil shear strength across dune age stages. The y-axis represents the vertical force (kg/cm^2) required to penetrate the soil (panel 'a') and the torque required (kg/cm^2) to disrupt the soil surface (panel 'b'). The color gradient darkens along with dune stage stability along the x-axis (low (moving), medium (semifixed), and high (fixed dunes) stability). The letters represent statistical significance based on a post-hoc test ($p < 0.05$)

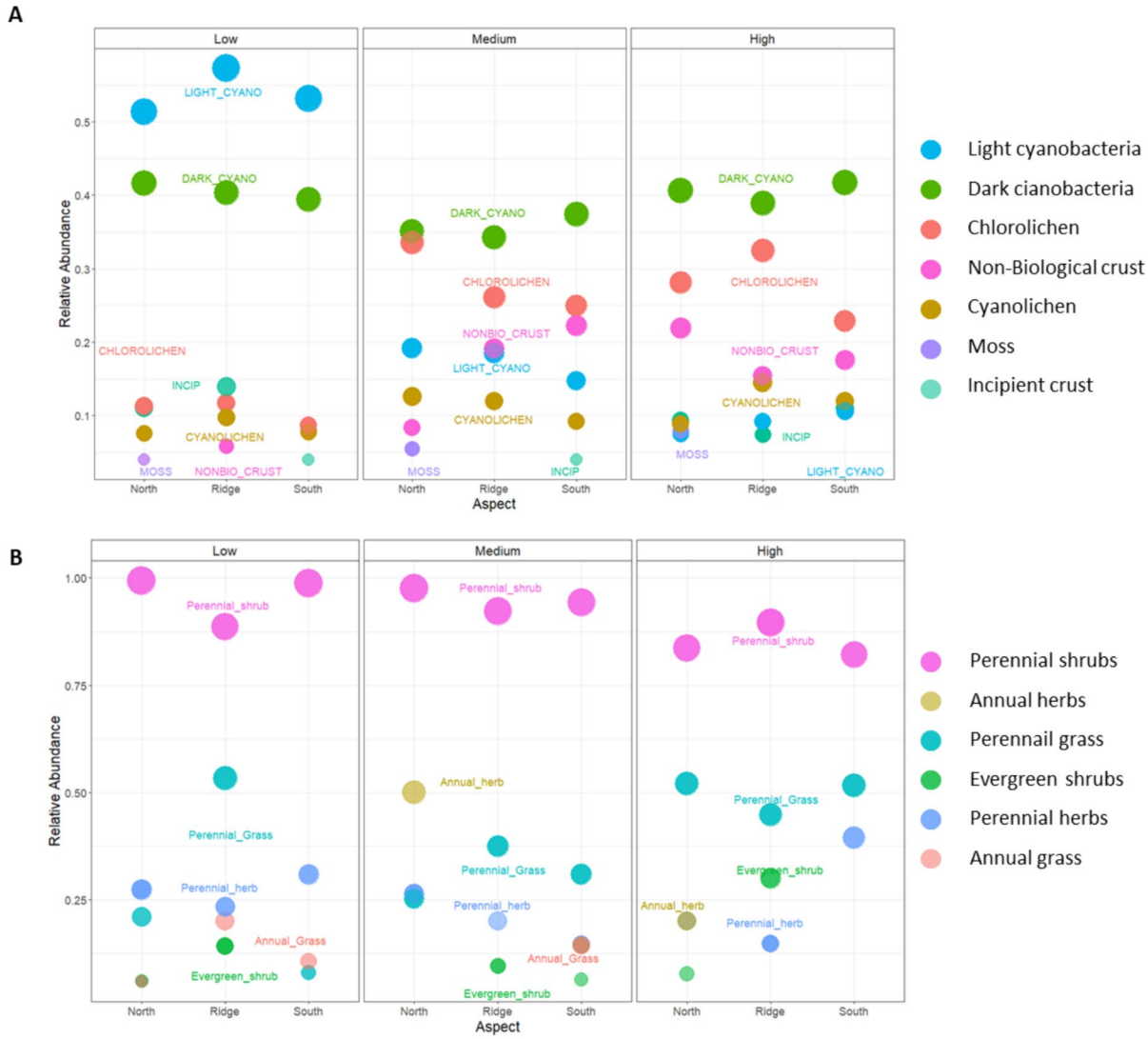


Fig. 3 Relative abundance of biocrust (**A**) and plant types (**B**) across stages and aspects of the dune edge. Biocrust types (**A**) considered were: incipient, light cyanobacteria, dark cyanobacteria, cyanolichen, chlorolichen, and moss. Vegetation types (B) considered were: perennial shrubs, perennial grasses, perennial herbs, evergreen shrubs, and annual herbs. The three different facets (grey labels) represent the three different levels of soil stability along the landscape gradient (low, medium and high stability). The y-axis and the size of the points represent the relative abundance for each biocrust type or vegetation type. The x-axis represents the slope-aspect at each soil stability stage

cover was similar across all aspects ($p > 0.05$, for all), while in the moving dunes, the ridge had significantly greater plant cover compared to the north- and south-facing aspects ($p < 0.001$). Plant community diversity was not significantly different ($F_{2,26} = 2.0$, $p = 0.16$) between the moving (1.2 ± 0.34), semifixed (1.2 ± 0.18), and fixed (1.0 ± 0.27) dunes. To understand how the composition of the plant community changes between sites, we calculate the relative abundance of different plant types at each site (Fig. 3B). The differences in the relative abundance of different types of plants in each of the dune stages were marginally significant (Pillai trace = 0.66, $F_{2,44} = 1.8$, $p = 0.08$).

Perennial shrubs were the dominant plant group across the soil stability gradient, at every dune stage (0.64 ± 0.16).

Influence of abiotic and biotic factors on biocrust

Effect of dune stage and aspect on biocrust types structure

The dune age stage had a significant effect on the structure of the biocrusts-types (PERMANOVA, $R^2 = 0.45$, $p < 0.001$) as did slope aspect (PERMANOVA, $R^2 = 0.02$, $p = 0.04$), while their interaction effect was not significant (PERMANOVA, $R^2 = 0.02$, $p = 0.16$).

Regarding the discriminant analysis, the first canonical axis explained 67.7% of variance, and the second canonical function 17.3% of the total variance (Fig. 4). The first canonical axis (Can1) separated the biocrust-type community in the different dune age stages, distinguishing between low-stability dunes—characterized by abundant light cyanobacteria—from more stable dunes, where lichen crusts (primarily chlorolichens, followed by cyanolichens) dominated (Fig. 4). The second canonical axis (Can2) distinguished between the slope aspects, where north-facing slopes were distinguished by greater moss abundance across all dune stages, whereas south-facing slopes were marked by more cyanolichens across all dune

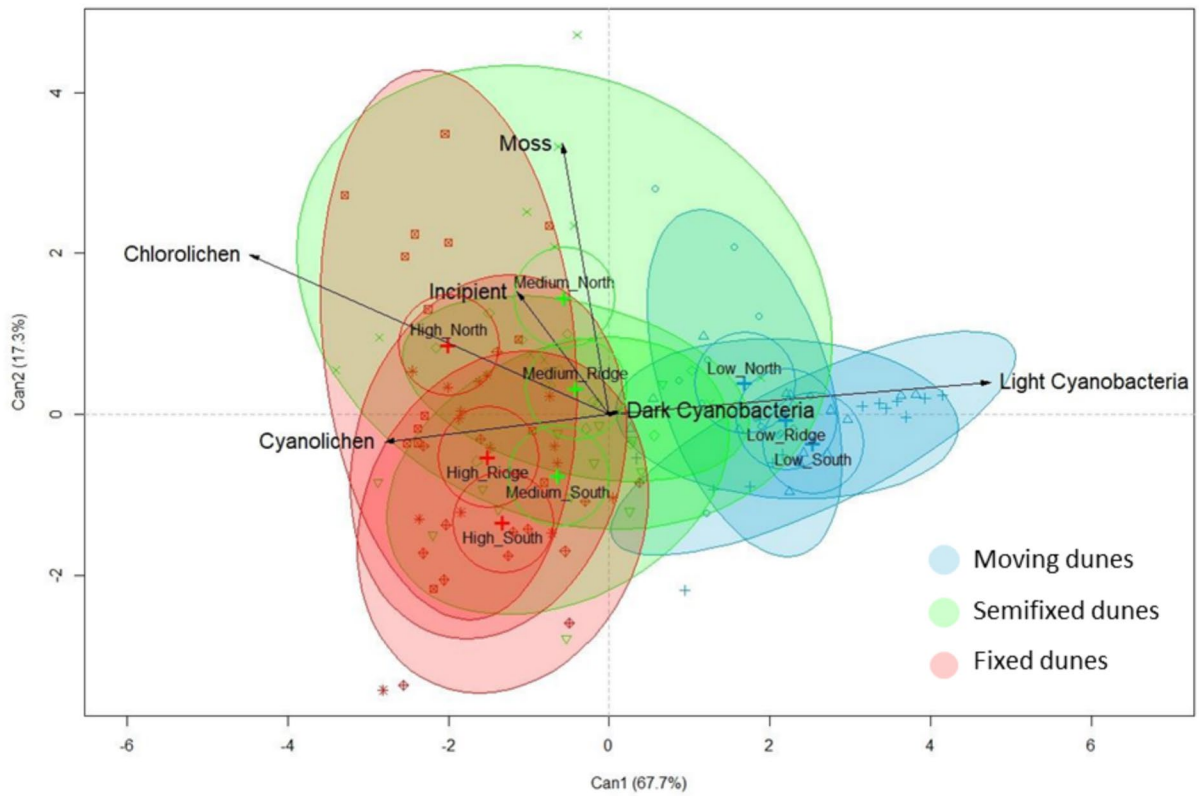


Fig. 4 Canonical scores of the first two canonical discriminant functions (Can1 & Can2) differentiating between the biocrust community composition based on the abundance of different biocrust community types throughout the soil stability gradient: low stability or moving dunes (blue), medium stability or semifixed dunes (green) and high stability or fixed dunes (red) and aspects (north, ridge, south). The first axis (Can1) explains 67.7% of the total variance and differentiates most strongly between the high abundance of light cyanobacteria crust in the low stability dune stage from the medium and high stability dune stages, which are defined by chlorolichen and cyanolichen crusts. The second axis (Can2) explains 17.3% of the total variance and differentiates between aspect slopes such that the north aspect is defined by moss crust across all dune stages

stages. On the ridge, cyanolichens dominated in low- and high-stability dune stages, while mosses prevailed in the medium-stability dune stage, making this community more similar to north-facing slopes (Fig. 4).

The influence of plant species identity on biocrust-type structure and its interaction with dune stage

Plant species had a significant effect determining the composition of biocrust-types (PERMANOVA, $R^2 = 0.08$, $p < 0.001$). The biocrust-type structure beneath the canopy of *Ephedra trifurca* was differentiated by a higher abundance of chlorolichen, moss and cyanolichen crusts while *Tiquilia hispidissima* and *Nerisyrena linearifolia* were more differentiated by incipient crust and light and dark cyanobacteria crusts, respectively (Fig. 5; Table S3). The CDA analysis showed that first canonical axis (Can1) account for 73.3% of the variance, separating the biocrust-type structure associated with *Ephedra trifurca* from that associated to *Tiquilia hispidissima* and *Nerisyrena linearifolia* (Fig. 5). Among all the variables, the abundance of chlorolichen crust contributed the most to this separation (i.e. to the first canonical axis), while dark cyanobacteria crust contributed the least (Fig. 5).

The relative abundance of various types of biocrust beneath the plant canopy versus paired

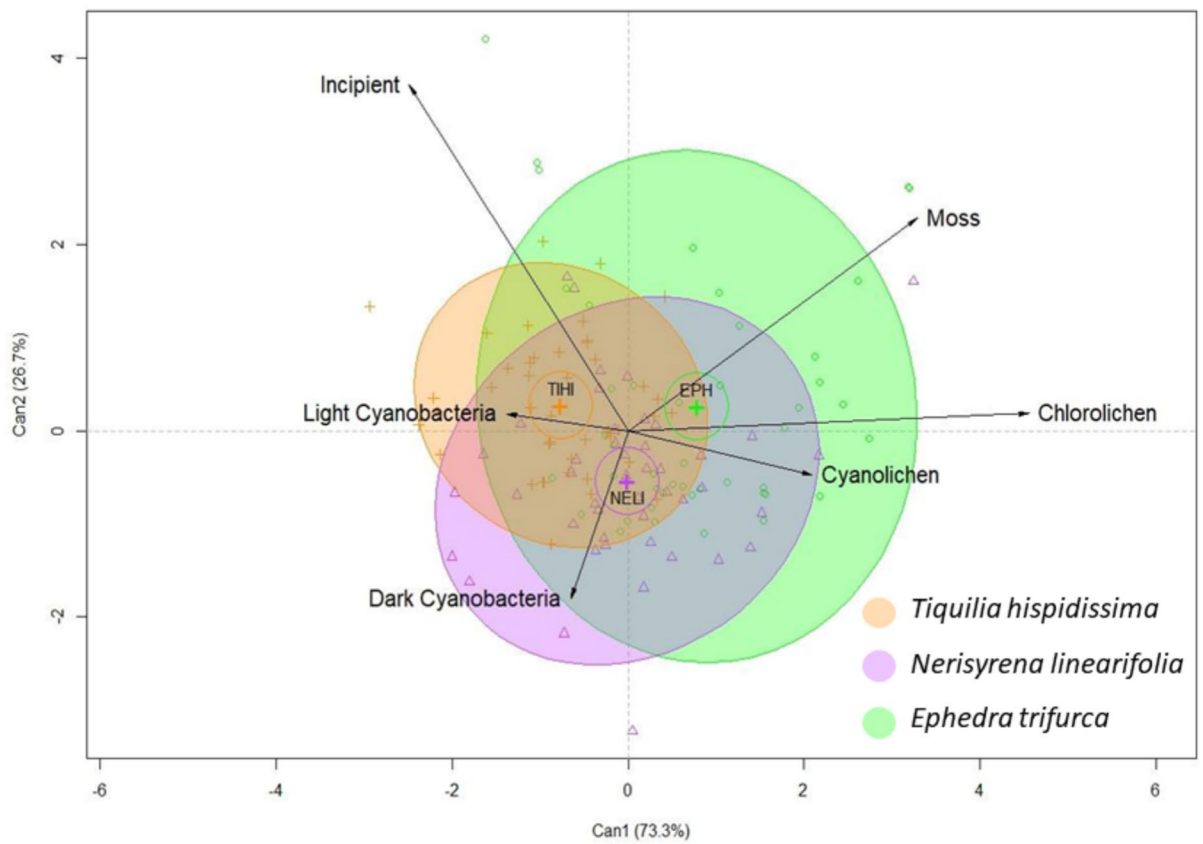


Fig. 5 Canonical scores of the first two canonical discriminant functions (Can1 & Can2) explaining the difference in abundance of crust community types under the plant canopy versus a paired interspace across species. The three different plant species are represented with different colors: Orange represents Tiquilia hispidissima (TIHI), purple for Nerisyrena linearifolia (NELI), and green for Ephedra trifurca (EPH). The first canonical function (Can1) explains 73.3% of the total variance and differentiates Ephedra trifurca, which is defined by chlorolichen, moss and cyanolichen from Tiquilia hispidissima, which is defined by a higher presence of the incipient crust and Nerisyrena linearifolia, which is more associated with dark and light cyanobaceteria crust

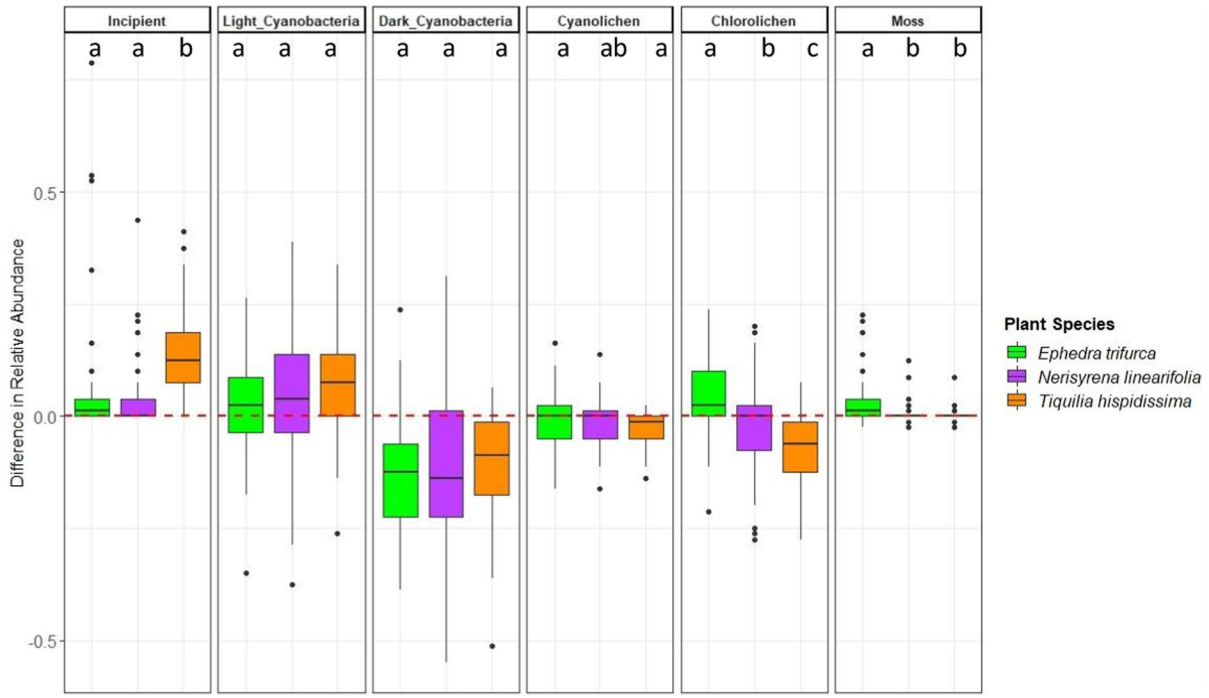


Fig. 6 *A box plot based on the difference in abundance of different biocrust types beneath the plant canopy compared to the paired interspace. Along the x-axis are the three different plant species: Ephedra trifurca* (green), *Nerisyrena linearifolia* (purple), and *Tiquilia hipidissima (orange).* The *y-axis represents the difference in relative abundance calculated by subtracting the relative abundance of each functional group present in the interspace from what was quantified below the plant. Each facet plot represents one of the main biocrust types we studied: incipient, light, and dark cyanobacteria, cyanolichen, chlorolichen, and moss (see the upper labels in the plot). Positive values indicate that the plant had a higher abundance, while negative values indicate that the interspace had a higher relative abundance (highlighted by the red dotted line). Different letters represent statistical significance between plant species (*$p < 0.05$*)*

interspaces differed significantly among plant species (Fig. 6; Table S4). *Tiquilia hispidissima* had a significantly weaker negative effect on the abundance of incipient crust beneath its canopy ($X^2_{2,135} = 46.4$, $p < 0.001$; estimated mean ± SE, -2.22 ± 0.28) compared to the other two plant species (*Ephedra trifurca*: -3.22 ± 0.31; *Nerisyrenia linearifolia*: -3.62 ± 0.32, $p < 0.001$ for both). The abundance of cyanolichen crust also significantly differed among plant species ($X^2_{2,135} = 7.0$, $p = 0.03$). *Tiquilia hispidissima* showed a significantly stronger negative effect (-0.03 ± 0.01) than *Ephedra trifurca*, where the abundance of cyanolichen below its canopy was more similar to its paired interspace soil surface (-0.003 ± 0.01, $p = 0.03$) (Table S4). However, the effect of *Nerisyrenia linearifolia* on cyanolichen crust abundance (-0.01 ± 0.01) did not differ from *Tiquilia hispidissima* ($p = 0.24$) or *Ephedra trifurca* ($p = 0.58$). The abundance of chlorolichen crust significantly differed across the three plant species ($X^2_{2,135} = 38.7$, $p < 0.001$) with *Ephedra trifurca* showing a significantly larger positive effect (0.04 ± 0.02) than both *Nerisyrena linearifolia* (-0.02 ± 0.02, $p = 0.003$) and *Tiquilia hispidissima* (-0.08 ± 0.02, $p < 0.001$). *Tiquilia hispidissima* showed a significantly stronger negative effect on chlorolichen abundance than *Nerisyrenia linearifolia* ($p = 0.01$). The abundance of moss crust also differed among plant species ($X^2_{2,135} = 30.6$, $p < 0.001$), with *Ephedra trifurca* showing a significantly greater positive effect (-3.64 ± 0.37) than *Tiquilia hispidissima* (-5.37 ± 0.48, $p < 0.001$) and *Nerisyrena linearifolia* (-5.53 ± 0.49, $p < 0.001$) (i.e. showed more moss crust beneath its canopy than on its paired interspace). In contrast, light cyanobacteria abundance was consistently higher under canopies across all species ($X^2_{2,135} = 2.9$, $p = 0.24$), with a greater

abundance of light cyanobacteria crust beneath the plant canopy compared to the interspace soil for all (Table S4). Conversely, dark cyanobacteria crust was consistently more abundant in interspaces, with differences across plant species ($X^2_{2,135} = 3.2$, $p = 0.20$; Table S4).

The interaction effect between the dune stage and the identity of the plant species was not significant (Pillai trace = 0.22, $F_{24,496} = 1.2$, $p = 0.22$). Thus, the influence of plant species identity on the structure of the biocrust-types was maintained throughout the dune stages.

Discussion

The structure of the biocrust types differ across a soil stability gradient

Our results show clear shifts in biocrust composition across the soil stability gradient. The establishment of early successional biocrust types is critical for the subsequent colonization of more structurally complex biocrusts such as dark cyanobacteria, lichen, and moss crusts. We show that low-stability, geomorphically young dunes showed a higher cover of light cyanobacteria crust, reflecting an early successional stage of biocrust development. Cyanobacteria are pioneer organisms in the establishment of biocrusts in nutrient-poor substrates, aided by the high degree of physiological plasticity, allowing them to tolerate extreme abiotic stress (Garcia-Pichel and Wojciechowski 2009). Filamentous light cyanobacteria, such as those belonging to the genera *Microcoleus, Trichocoleus, Schizothrix* and *Coleofasciculus,* are known to improve soil aggregate ability as they secrete sticky exopolysaccharides that form interconnected mats within the soil, enhancing soil stabilization (Mazor et al. 1996; Issa et al. 2001; Mühlsteinová et al. 2014; Chamizo et al. 2018). Such dynamics are consistent with previous work showing that dune stabilization promotes the rapid formation of incipient crusts (Kidron et al. 2000; Fang et al. 2007) and that cyanobacteria strongly influence soil physicochemical properties and plant regeneration (Lan et al., 2014). The stabilizing ability of early successional light cyanobacteria crusts could interact with dune hydrology, lowering the risk of evaporation in sandy soils (Kinraide 1984; Grigg et al. 2008; Kidron et al., 2000), and interact with sediment hydrology, and the establishment of vascular plants further reducing dune mobility (Thompson and Moore 1984). Our results are in line with this previous work considering that the low stability dune stage represents the most recently demobilized dune stage, so a greater abundance of light cyanobacteria versus later successional biocrust types is expected.

As stability increased and plant cover declined, we observed a shift toward structurally complex biocrusts, particularly lichens and mosses, consistent with the successional trajectory reported in earlier studies finding that these macroscopic organisms can be established in the community only after the substrate has been colonized and stabilized by cyanobacterial crusts (Lange et al. 1992; Garcia-Pichel et al. 2001). In contrast to Soliveres and Eldgridge (2020), we observed an increase in biocrust-types richness as plant cover decreased, potentially driven by an increase in a reduce-vegetation surface with less competition over resources such as nutrients and light (Belnap et al. 2001; Buis et al. 2009; Ding and Eldridge 2020). The later successional biocrust types not only enhance soil stability but also contribute to nitrogen and carbon fixation (Hoellrich et al. 2023), highlighting their importance for nutrient cycling and ecosystem productivity (Li et al. 2016; Gao et al. 2017; Liu et al. 2016; Oliveira et al. 2022). Therefore, deepening an understanding of how to predict the distribution of these more energy-efficient biocrust types has important implications for hydrological patterns and ecosystem functioning.

Dune age, soil stability, and aspect affected biocrust community structure

We found that biocrust communities on the north facing slopes had the highest moss cover across all three soil gradient sites, which is consistent with previous findings showing that the development of mosses is strongly restricted by low soil moisture levels (Martínez-Sánchez et al. 1994) and thus tend to occur more on moist substrates or shaded microhabitats (Zhou et al. 2020; Bowker et al. 2005; Maestre et al. 2002; Pietrasiak et al. 2011). The water status of mosses is completely dependent on water available in the environment, and given the absence of water-transporting roots, they rely on above-ground structures for water absorption and storage. Mosses can be particularly

sensitive to changes in individual rain events, particularly small rain events, which can induce rapid drying desiccation stress and do not allow mosses to fully rehydrate, but may initiate activity nonetheless, which can lead to C starvation (Barker et al. 2005; Reed et al. 2012; Schwinning et al. 2004). Despite adaptations for desiccation protection such as a rehydration-induced repair system to physiologically recover from reduced moisture (Oliver et al. 2000), the ability to utilize dew and fog as water sources (Pan et al. 2016), and physically 'rolling up' while drying to protect sensitive photosynthetic tissue (Frey and Kürschner 1991), our findings indicate that moss crusts benefit from microclimatic conditions that slope orientation influences, as they are greater in abundance on the north aspect which has a microclimate of reduced solar radiation, and consequently reduced desiccation stress.

Interestingly, while the three slope positions (north, ridge, and south) followed a similar trend in the composition of the biocrust-types across soil stability stages, there is less differentiation between the biocrust-types communities in different slope aspects in the low stability dune stage compared to the more stable dune stages, where the biocrust-types communities in different slope aspects are more distinct. All three slope positions (south facing, north facing, ridge) in the low stability dunes were more similar in composition than the other dune stages (Fig. 3, 4) and were dominated by light cyanobacteria crusts (Fig. 3). Despite the soil stabilization that light cyanobacteria crusts perform, early successional cyanobacterial crusts have overall lower biomass, providing less strength and resistance against erosion (Belnap et al. 2001), which could make light cyanobacteria-dominated sandy soils more susceptible to relocation from wind activity transporting the upper soil layer. Additionally, many of the cyanobacteria found within light cyanobacteria crust exhibit gliding motility, allowing them to move through substrates both vertically, to avoid extreme abiotic stress, as well as laterally, to disperse and explore the soil matrix and surface (Garcia-Pichel and Pringault 2001; Pringault and Garcia-Pichel 2004). Thus, the motility of the cyanobacteria themselves could enable more movement between slope aspects, as they are capable of relocating after light sand burial (Belnap and Eldridge 2001), accounting for less differentiation in biocrust-types community across slope-aspects in the low stability dune.

As expected, cyanolichen crusts were more associated with the south-facing slope, while chlorolichens were more associated with the north facing aspect. Rodríguez-Caballero et al. (2022) found that both moss and chlorolichen dominated crusts were positively correlated with precipitation and negatively correlated with temperature. Thus, less intense UV radiation on the north facing aspect could reduce water loss to evaporation and experience less extreme temperature increases than on the south facing aspect, which could explain the prominence of chlorolichens observed on the north-aspect. Our finding that cyanolichens are more prominent on the south facing aspect could be a consequence of greater competition for light and space with plants and other biocrusts on the north facing aspect, which was the most colonized by moss whose growth forms can restrict available space for other biocrusts to colonize.

Cyanolichens, though able to use low light intensities under plant canopies (Rikkinen 1995), still compete with vascular plants for photosynthetically active light (Armstrong 1991). Their reliance on liquid water for photosynthesis, unlike chlorolichens that can use dew or vapor (Lange et al. 1986), suggests adaptation to more arid environments. Indeed, cyanolichens have been linked to sites of higher aridity (Matos et al. 2015; Rogers 2006), aided by protective compounds against high irradiance, such as scytonemin produced by their cyanobacterial photobionts (Büdel et al. 1997; McEvoy et al. 2007). This dark pigmentation may explain their greater abundance in drier, high-insolation habitats (Zedda et al. 2011). Moreover, photobionts within functional thalli (in symbiosis with a lichen) show enhanced stress tolerance compared to isolated cultures (Kranner et al. 2005). These adaptations align with our finding that cyanolichens are more abundant on the south-facing slopes, where exposure and aridity are greater, than on the north-facing slopes.

Additionally, lichens exhibit high levels of plasticity in their responses to high light stress. The same lichen species can develop distinct 'sun' or 'shade' forms to live on both north and south facing slopes, reflecting adaptive strategies to contrasting microhabitats (Green et al. 1997; Pintado et al. 1997, 2005; Veres et al. 2020). The range of distribution that

some biocrusts can display reflects potential thresholds and adaptations they could exhibit in scenarios of increased abiotic stress. Such plasticity and wide distribution ranges highlight the potential thresholds and adaptive responses biocrusts may display under increasing abiotic stress, with important implications for predicting shifts in biocrust community structure and ecosystem functioning under future climate scenarios.

Different plant species are associated with different types of biocrust

Differences in plant species morphology (i.e., canopy and leaf structure, plant root system) shape diverse microenvironments (i.e. temperature, moisture, and nutrient availability) that influence which types of biocrusts are favored. Our results show that *Ephedra trifurca* was associated with chlorolichen and moss biocrusts. Desert shrubs like this are known to improve stressful environmental conditions, providing a 'refuge' beneath their canopy with increased soil nutrients and increased soil moisture through hydraulic lift (Filazzola and Lortie 2014; Cantón et al. 2004). Despite being well adapted to harsh abiotic conditions, it has been shown that certain later successional biocrusts can benefit from a shading effect that plants provide which can reduce evapotranspiration and buffer temperature extremes (Martínez-Sánchez et al. 1994; Maestre et al. 2002; Li et al. 2005). Its deep root system extracts soil water from depths > 1.95 m (Yoder and Nowak 1999), but with an inefficient acquisition of shallow soil water (Bleby et al. 2010; Caldwell et al. 1998). Of the three plant species we considered in this study, *Ephedra trifurca* had the average tallest height (Table S2) and thus likely provides a more substantial shade effect which could moderate increases in soil surface temperature and consequently reduce water loss due to evaporation (Potts et al. 2010; Hennessy et al. 1985; Kidron 2009), creating conditions that support later-successional biocrusts.

In contrast, *Tiquilia hispidissima* was most associated with incipient crust. Its low and wide canopy with bristly herbage generates a dense canopy that blocks incoming light preventing the establishment under-story plants (Carrillo-Garcia et al. 1999) and the development of biocrusts, thus constraining carbon fixing capacities of biocrust constituents (Harel et al. 2004). Its main stems lined with clusters of linear leaves covered in small hairs, often graze the soil surface allowing the development of incipient crust in the fine sand texture (Pietrasiak et al. 2011), but preventing subsequent colonizers (i.e., dark cyanobacteria, lichen, and moss crusts) from forming. *Tiquilia hispidissima* also had the highest abundance of woody litter around the canopy compared to *Ephedra trifurca* and *Nerisyrena linearifolia* (Table S2). It has been shown that biocrust burial by accumulated woody litter restricts biocrust development under plant canopies (Berkeley et al. 2005; Ding and Eldridge 2020), which supports our findings of less developed biocrusts under the canopy of *Tiquilia hispidissima*.

Nerisyrena linearifolia was more associated with cyanobacterial crusts, particularly dark cyanobacteria. Early successional cyanobacteria crusts are light in color and have little UV-protective pigmentation (Belnap et al. 2001), while later successional dark cyanobacteria crusts are darker in color due to the presence of sunscreen pigments that protect them from UV radiation damage. *Nerisyrena linearifolia* have more narrow linear leaves and a shallower root system (rhizomatous) compared to other *Nerisyrena* species (i.e., *N. camporum*), which are taprooted and have broader leaves (Bacon 1978). The absence of a deep taproot system in *Nerisyrena linearifolia* may restrict their ability to increase soil moisture in their microenvironments via hydraulic lift, compared to more deeply rooted plants (Bleby et al. 2010; Caldwell and Richards 1989). Consequently, it provides little amelioration of factors inducing stress such as light radiation, temperature, and moisture levels, in line with our results showing that it favors stress-tolerant cyanobacteria crusts but not sensitive moss and lichen biocrusts.

Across species, light cyanobacteria (lacking UV-protective pigments) were more abundant under canopies, while dark cyanobacteria dominated interspaces, reflecting fine-scale heterogeneity in microhabitats. Although we did not measure specific environmental variables beneath each plant, our results demonstrate that plant species create distinct microenvironments that shape biocrust community structure. Future studies should explicitly test which canopy-related factors (e.g., temperature,

humidity, or soil moisture) drive these differences and also how the structure of biocrust-types can in turn affect the plants growth, and their nutritional status, that can in turn affect the micro-environment. Together, these results highlight how plant functional traits drive microscale variation in biocrust community structure that may interact with other spatial heterogeneity at the landscape scale related with soil stability.

Species-specific plant effect on biocrust-types structure is maintained across the soil stability gradient

Our findings highlight that plant species mediate biocrust-types composition in ways that remain stable even under varying soil stability. Previous studies have found that disturbances provoke different effects depending on biocrust community type (Escolar et al. 2012; Reed et al. 2012; Fernandes et al. 2018; Finger-Higgens et al. 2022). Showing that the effect of plant species on different biocrust types is maintained across a landscape which varied significantly in soil stability, texture and chemistry provides a knowledge that can guide conservation and restoration by linking plant species to the protection of different biocrust types as it has been previously proposed (Condon et al. 2020). Considering that once disturbed, biocrusts show a slow recovery that can last up to decades (Belnap et al. 1994), enhancing this recovery with selected plant species may contribute to safeguarding the multifunctionality that microbial diversity provides in dryland ecosystems (Delgado-Baquerizo et al. 2016).

Conclusions

Our results show that both plant species identity and geomorphology shape biocrust-types composition, and emphasizes the need to consider interactions between different abiotic factors, such as soils stability and slope, as biocrust types differ in their environmental requirements. This insight can be useful both for informing management actions, such as dryland restoration strategies and for improving predictions of climatic impacts on biocrust types and therefore their impact in ecosystem functioning.

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Author contributions Sarah Collins, Alicia Montesinos-Navarro, and Nicole Pietrasiak conceived the ideas and designed methodology; Sarah Collins and Nicole Pietrasiak collected the data; Sarah Collins and Alicia Montesinos-Navarro analyzed the data; Sarah Collins wrote the first draft of the manuscript. All authors contributed critically to drafts of the manuscript.

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Data availability The datasets generated during and/or analysed during the current study will be made available upon confirmation of publication of this article in the zenodo repository.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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