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RESEARCH ARTICLE

Soil cover heterogeneity associated with biocrusts predicts patch-level plant diversity patterns

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Abstract
Context Soil resource heterogeneity drives plant species diversity patterns at local and landscape scales. In drylands, biocrusts are patchily distributed and contribute to soil resource heterogeneity important for plant establishment and growth. Yet, we have a limited understanding of how such heterogeneity may relate to patterns of plant diversity and community structure.
Objectives We explored relationships between biocrust-associated soil cover heterogeneity and plant diversity patterns in a cool desert ecosystem. We asked: (1) does biocrust-associated soil cover heterogeneity predict plant diversity and community composition? and (2) can we use high-resolution remote sensing data to calculate soil cover heterogeneity metrics that could be used to extrapolate these patterns across landscapes?
Methods We tested associations among field-based measures of plant diversity and soil cover heterogeneity. We then used a Support Vector Machine classification to map soil, plant and biocrust cover from sub-centimeter resolution Unoccupied Aerial System (UAS) imagery and compared the mapped results to field-based measures.
Results Field-based soil cover heterogeneity and biocrust cover were positively associated with plant diversity and predicted community composition. The accuracy of UAS-mapped soil cover classes varied across sites due to variation in timing and quality of image collections, but the overall results suggest that UAS are a promising data source for generating detailed, spatially explicit soil cover heterogeneity metrics.
Conclusions Results improve understanding of relationships between biocrust-associated soil cover heterogeneity and plant diversity and highlight the promise of high-resolution UAS data to extrapolate these patterns over larger landscapes which could improve conservation planning and predictions of dryland responses to soil degradation under global change.

Keywords Biocrust · Soil heterogeneity · Plant diversity · Unoccupied Aerial Systems · Unoccupied Aerial Vehicles

Introduction

Environmental heterogeneity is often an important driver of biological diversity within ecological

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communities at local scales (Wiens 1976; Turner & Chapin 2005; Stein et al. 2014). Soil heterogeneity, broadly defined as the variability in soil properties and/or soil taxonomic classes within a given area (McBratney and Minasny 2007), is widely predicted to increase local plant community diversity (or alpha diversity; Whittaker 1960) by promoting plant coexistence through niche differentiation (Hutchinson 1957; Levine & HilleRisLambers 2009; Williams & Houseman 2014). Experiments testing the role of soil heterogeneity in plant diversity have often manipulated soil physical properties and nutrient levels. These studies have generated inconsistent results (e.g., Stevens & Carson 2002; Wijesinghe et al. 2005; Reynolds et al. 2007; Williams & Houseman 2014). Our understanding of this relationship remains limited due to the contradiction between theory and small-scale experiments, and variability in the relationship across spatial scales (Tamme et al. 2010).

In Earth's arid and semiarid (dryland) ecosystems, soil resources (i.e., water, nutrients) are heterogeneously distributed in space and time through patch and pulse dynamics (Schlesinger et al. 1996; García-Palacios et al. 2011; Collins et al. 2014) in which biological activity occurs in "pulses" following wetting events that punctuate intermediary periods of inactivity when soil water is scarce (Noy-Mier 1973). Dryland soil resource heterogeneity is further modified by biotic patterns and processes. Biological soil crusts (biocrusts)—surface-dwelling soil biotic communities comprised of cyanobacteria, algae, fungi, lichens, bryophytes (Weber et al. 2022)—occur in patchy mosaics on the soil surface and play critical roles in determining dryland soil resource heterogeneity at local scales (Belnap 2003; Concostrina-Zubiri et al. 2013). For example, biocrusts substantially modify soil hydrology (Eldridge et al. 2020), and relative to bare soil, generally increase soil stability, microtopography (Caster et al. 2021), and moisture (Eldridge et al. 2020), and promote soil nutrient availability by fixing atmospheric nitrogen (Barger et al. 2016) and carbon (Mastre et al. 2013), excreting organic compounds and chelate mineral elements into the soil surface (Harper & Pendleton 1993), and trapping nutrient-rich fine dust particles (e.g., Martínez et al. 2006; Delgado-Baquerizo et al. 2010).

Due to the patchy distribution of biocrusts within drylands (Kozar et al. 2024), and the diversity and spatial organization of organisms within biocrust communities (Weber et al. 2022), biocrusts directly generate soil cover heterogeneity with implications for soil functioning. Yet, despite such contributions to soil cover heterogeneity (Concostrina-Zubiri et al. 2013; Bowker et al. 2014), biocrusts have historically been examined as single units within ecosystems rather than as biologically and spatially complex communities (Maestre et al. 2005). Nonetheless, exploring biocrust contributions to spatial soil cover and associated resource heterogeneity may be fundamental to understanding dryland ecosystem functioning and diversity patterns at local to landscape scales (Maestre et al. 2005) including biocrust interactions with plants and broader ecosystem patterns and processes. Biocrust-mediated soil cover heterogeneity may have important implications for vascular plant community composition and distribution. Biocrusts can have multifaceted yet variable impacts on plant recruitment, growth, and survival (Havrilla et al. 2019), and as such, may have important filtering effects on plant assemblages (Bowker et al. 2022; Havrilla et al. 2019; Luzuriaga et al. 2012; Oritz et al. 2023). Plant responses to biocrusts vary depending on plant species and functional traits and biocrust community composition (Havrilla et al. 2019; Oritz et al. 2023). Plant species differ in their ability to establish alongside biocrust patches, thus creating preferential niches and diverse biogenic communities (Hutchinson 1957). Though, the few studies that have examined the effects of biocrusts on plant diversity and community composition have generated mixed results whereby biocrusts have been shown to have positive (Kleiner & Harper 1977; Jeffries & Klopatek 1987; Luzuriaga et al. 2012; Scott & Morgan 2012) or negative (Peralta et al. 2016; Miller & Damschen 2017) effects on plant diversity patterns. Overall, the potential of biocrust-associated soil cover heterogeneity to explain patterns in plant diversity at patch and landscape scales remains underexplored.

Given the significant contributions of biocrusts to spatial heterogeneity and ecological processes in drylands, it is important to understand their distribution and abundance at landscape scales (Rodríguez-Caballero et al. 2015; Ferrenberg et al. 2017; Smith et al. 2019). Yet, biocrusts are susceptible to local disturbances such as trampling by animals and humans (Zaady et al. 2016). Consequently, using ground-based monitoring techniques to survey and map biocrusts can be destructive to biocrust communities.

However, since biocrust biomass and biological activity is generally concentrated and visible in the uppermost millimeters of the soil surface (Garcia-Pichel et al. 2003), remote sensing provides alternative opportunities to detect and characterize biocrust communities without physical soil disturbance.

Remote sensing has proven an effective tool for characterizing and scaling biocrust patterns and assessing their ecological function (Read et al. 2016; Rodríguez-Caballero et al. 2015; Weber and Hill 2016). Recent advances in biocrust remote sensing using small Unoccupied Aerial Systems (UAS) show potential for characterizing biocrust cover, patch dynamics, and heterogeneity at ecologically relevant scales (Havrilla et al. 2019; Kozar et al. 2024) and may thus present promising tools for exploring relationships between biocrust-mediated ground cover and ecosystem patterns including plant diversity. UAS can provide mapping at scales between field studies and satellite imagery and may provide an optimal spatial resolution for detecting biocrusts and characterizing their spatial patterns (Havrilla et al. 2019). Biocrusts can vary widely in appearance and spectral reflectance, making it difficult to apply spectral training data across sites. New deep learning approaches have shown promise for accurate segmentation and classification of biocrusts from very high-resolution photography (Herdy et al. 2024) and show promise for cross-site image models. To date, most of the UAS-based remote sensing of biocrusts have used true-color RGB imagery (Havrilla et al. 2019; Collier et al. 2022; Kozar et al. 2024) exploiting differences in image brightness and texture between biocrusts, soil and vegetation cover, with some investigations into thermal-IR and hyperspectral imaging (Smith et al. 2019; Blanco-Sacristán et al. 2021). UAS remote sensing has been generally underutilized in landscape ecology research (see Villarreal et al. 2024) but has proven effective for assessing plant and soil dynamics and spatial patterns (Getzin et al. 2022; Rodríguez-Lozano et al. 2023), predicting local-scale plant diversity (Polley et al. 2019) and for linking structure and function across sites and landscapes (Cunliffe et al. 2022).

To investigate potential relationships between soil cover heterogeneity associated with biocrusts and herbaceous plant diversity, we conducted an observational field study in a cool desert ecosystem within the Colorado Plateau ecoregion of the western United States using field-based surveys and UAS-based remote sensing. We hypothesized that biocrusts increase local plant alpha diversity (i.e., species richness, Shannon diversity) by increasing fine-scale spatial soil heterogeneity and promoting plant coexistence through niche differentiation. We addressed the research questions: (1) is biocrust-associated soil cover heterogeneity associated with local plant diversity and/or community composition? and (2) can we use high-resolution remote sensing data to calculate soil cover heterogeneity metrics that could be used to extrapolate these patterns across larger landscapes? Rather than being conducted under heavily controlled experimental conditions like many soil heterogeneity-plant diversity studies, this study was conducted in an area where active livestock grazing contributes to patterns of soil cover heterogeneity, biocrust cover, and plant diversity on the landscape. Such an approach is valuable for determining soil cover heterogeneity-plant diversity patterns in situ in the context of land use and global change.

Materials and methods

Study site

The study area is located in Beef Basin in Southeastern Utah, USA, within the Colorado Plateau Ecoregion (Lat 37° 58’ N, Lon 109° 56’ W). Beef Basin is located within the Bureau of Land Management’s (BLM) Indian Creek grazing allotment that borders Canyonlands National Park to the south and southeast (Fig. 1). Regional climate of the study area is semiarid with a mean annual precipitation of 335 mm (range = 142–474 mm/year), and a mean annual temperature of 11.6 °C (PRISM Climate Group 2014; 30-year average, 1981–2010). Mean site elevation is 1882 m, and soils are characterized taxonomically as Loamy, mixed, superactive, mesic Lithic Haplocambid (Leanto fine sandy loam; Web Soil Survey 2018). The main land uses of the area are cattle grazing (November—May) and recreation. We focused our survey on Semidesert Shallow Loam (Black Sagebrush/Indian Ricegrass) ecological sites within the study area dominated by *Artemisia nova* (A. Nelson; black sagebrush) and perennial grasses *Achnatherum hymenoides* (Roem. & Schult.; Indian ricegrass), *Pleuraphis jamesii* (Torr.; James’ galleta), and

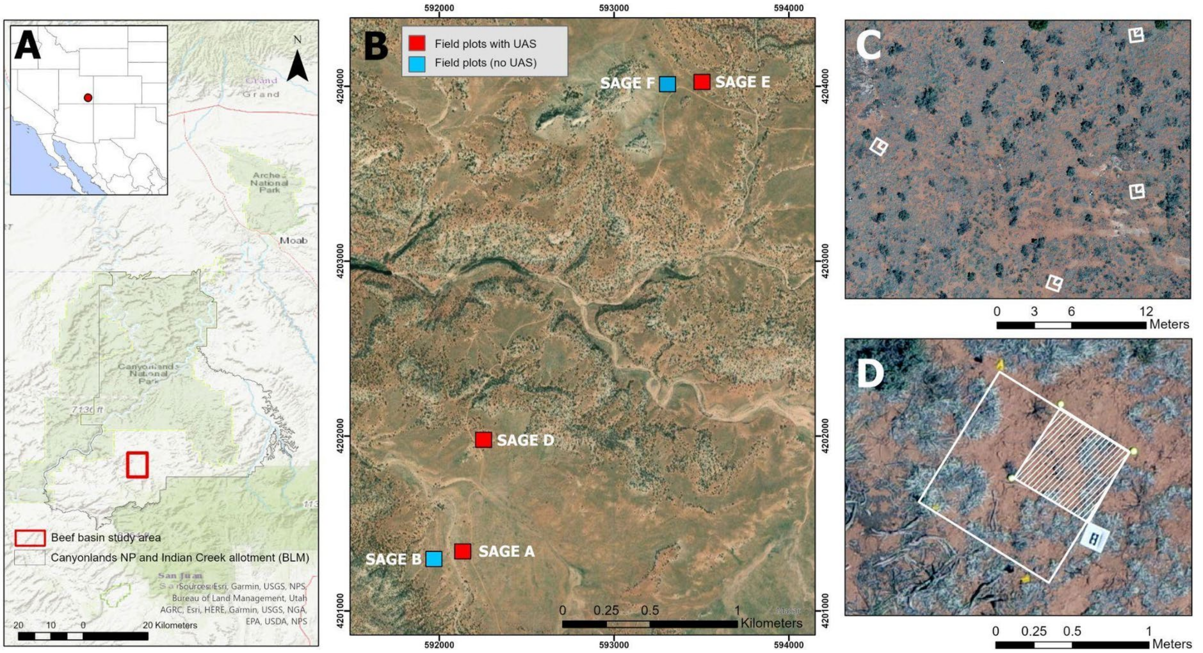


Fig. 1 **A** Map of the Beef Basin study area in southeastern Utah, USA. **B** UAS data were collected at three, 50 × 50-m plots in the study area (red rectangles) and field data were collected at five plots total, including UAS plots (Sage A, D, and E) and two plots (Sage B and F) without UAS (blue rectangles). **C** Example layout of field patches (white) within a plot, and **D** zoom of individual patch and 1-m^2 vegetation quadrats outlined in white and 0.5-m^2 soil quadrats ("patches") hatched in white

Bouteloua gracilis (Willd. and Kunth; Blue grama; Web Soil Survey 2018).

In June 2018, we established five, 50 × 50-m (0.25 ha) observational field plots. Within each, we established eight, nested subplots (hereafter "patches") to measure cover and community composition of biocrusts (0.5-m^2) and herbaceous plants (1-m^2) for a total of 40 patches. Patches were positioned randomly in open areas within plots (i.e., areas not covered by shrub or tree canopies) but at least five meters apart and represented a gradient of biocrust cover. We focused our investigations on the herbaceous plant community (rather than herbaceous and woody because herbaceous plant species, in general, have shallow root systems and shorter lifespans than woody plants and thus may be more sensitive to biocrust-mediated soil resource variation at the soil surface (Kidron & Aloni 2018). Woody plants also influence nutrient distributions that can affect biocrust and plant distributions (Ravi and D'Ordorico 2009; Ju et al. 2021). We assigned a qualitative metric of grazing level (i.e., low, medium, high) to each plot based on field estimates of the average observed number of hoofprints present within a five randomly selected 10-m^2 areas within each plot (0–5 = low, 5–10 = medium, > 11 = high) in an effort to characterize differences in livestock utilization across plots.

Field-based soil cover and soil heterogeneity measures

In each patch, we used a 0.5-m^2 quadrat with 100 intersects to measure the percent cover of soil cover classes (Table 1, Fig. 2). Soil data from each patch were analyzed using a multi-metric approach to describe soil heterogeneity. First, we calculated the percent cover of all soil cover classes. Then, using these soil cover data, we used land cover heterogeneity metrics commonly used in larger-scale spatial landscape analyses: Land Cover Richness, Land Cover Diversity to quantify metrics of fine-scale soil cover heterogeneity at the patch level: (1) soil cover richness (SCR): the total number of different soil cover classes present within the sampling area; and

Table 1 Descriptions of soil predictor variables: field-based soil cover classes, metrics of soil heterogeneity (e.g.,SCH), and other patch characteristics

Variable	Description
Soil cover classes	
Bare soil cover (%)	Soil without biocrust organisms present (i.e., bare soil, physical soil crust, and/or rock or gravel)
Dark biocrust cover (%)	Biocrusts dominated by cyanobacteria, mosses, and lichens—dark in coloration
Light biocrust cover (%)	Biocrust dominated by cyanobacteria*—light in coloration
Non-photosynthetic vegetation (NPV) cover (%)	Non-photosynthetic vegetation materials on the soil surface (e.g., litter, duff, and wood)
Soil heterogeneity metrics	
Soil cover richness (SCR)	Number of soil cover classes present within the patch (range: 1–4)
Soil cover heterogeneity (SCH)	Shannon diversity (H) of soil cover classes present within the patch
Other plot characteristics	
Soil depth (cm)	Depth of soil to the top of the C horizon taken outside top right corner of the patch (cm)
Plot elevation(m)	Mean plot elevation(m)
Grazing intensity	Plot grazing intensity (low, medium, high)

Cover of soil classes determined using quadrat sampling methods in 0.5-m^2 soil patches. *Whether ground cover was classified as "Bare Soil" or "Light biocrust" was determined by taking a small sample of soil adjacent to the sampling quadrat. Soils that fell apart immediately with no visible cyanobacterial filaments were labeled "Bare Soil," and soils that stuck together, with visible cyanobacterial filaments present (but without dark pigmentation or accompanying mosses and/or lichens) were labeled "Light Biocrust."

(2) soil cover heterogeneity (SCH): calculated using the Shannon–Wiener diversity index ($H = -\Sigma Pi(\ln Pi)$; Shannon & Weaver 1949) where p_i is the proportion of each soil cover class (see Table 1) within the plot. These metrics were chosen due to their widespread use in spatial landscape analysis and effectiveness in quantifying environmental spatial patterns (Peng et al. 2010; Plexida et al. 2014).

Field-based herbaceous plant cover and plant species diversity

For all patches, we also quantified herbaceous plant community composition using 1-m^2 vegetation quadrats. We used a 1-m^2 quadrat with 100 intersects to measure percent cover and abundance of herbaceous plant species by dropping a pin flag and recording all plant canopies down to the soil level. Herbaceous plant species identified in Beef Basin study plots are provided in Table S1 (USDA NRCS 2024). Plant species that could not be identified in the field were collected and identified in the herbarium at the University of Colorado Boulder. Fewer than 5% of unknown species specimens encountered could not be identified due to phenological stage or missing floral parts. In these cases, plants were identified to the genus level and treated as individual species. Then, plant census data were used to calculate herbaceous plant richness and diversity.

Remotely sensed measures of soil cover heterogeneity

Three band true-color (red, green, blue; RGB) image data were collected on June 2, 2018, using a Ricoh GR II camera (18.3 mm lens) mounted on a 3DR Solo quad-rotor aerial vehicle. We processed data for three plots covering approximately 0.25 ha each (Fig. 1). Flights were conducted at 11:15, 15:15 and 15:45 MDT at altitudes ranging from 13.6 to 22.4 m, resulting in ground sampling distance of 0.47, 0.33, and0.56 cm for plots Sage A, D and E respectively. Details on image processing and other metadata can be found in Havrilla et al. (2019). Two UAS orthomosaics collected at sagebrush sites and included in Havrilla et al. (2019) were not used in this study due to image inconsistencies in the mosaicked products that might have affected pixel-based supervised classifications based on limited training samples. All image data and derived products used for this study can be found in Villarreal and Havrilla (2024).

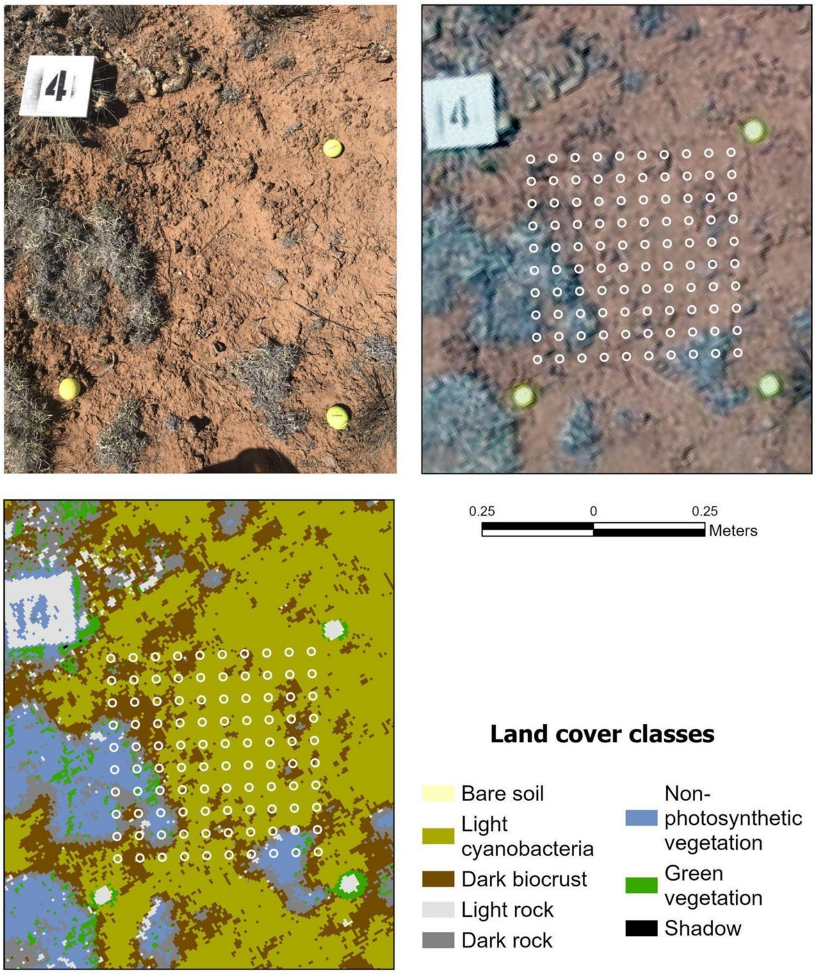


Fig. 2 Field photograph of patch-level 0.5-m^2 quadrat (top left) used to measure soil cover classes, next to UAS image of same plot (top right) showing approximate locations of 100 intersects (labeled as white circles in top figure) that were used to measure the cover of soil cover classes in the field. Corners of patches were labeled and marked to be visible in the aerial imagery (top right). We used the 100 intersect markings to extract % cover information from the classified images (bottom) and to evaluate the image products

Support vector machines image classification

We used support vector machines (SVMs), a supervised, non-parametric classifier to classify the sub-centimeter 3-band RGB imagery into the following classes: dark biocrust, light biocrust, bare soil, dark rock, light rock, green vegetation, non-photosynthetic vegetation (NPV), and shadow. For each image area we selected 25–35 training regions of interest (ROIs) per class, which were manually digitized over the orthoimagery. ROI selection was aided by geolocated ground photographs collected in June 2018 during the field and UAS campaigns. Previous research on very high resolution biocrust mapping in these plots (Havrilla et al. 2019) applied an object-based mapping approach with SVM classification, but we chose a pixel-based SVM here in order to capture the fine-scale variation in soil cover types that were measured within the 1-m^2 field subplots (~100-point intercept records). SVM models used a Radial Basis Function kernel (non-linear), selecting 0.333 Gamma, based on number of bands, 0.75 penalty parameter (i.e., trade-off between complexity and the number of non-separable points) and classification probability threshold (i.e., probability required to classify a pixel) = 90.

Remotely sensed soil cover heterogeneity

We calculated remotely sensed soil cover heterogeneity (SCH_RS) on rasters reclassed to represent the three main soil cover classes: bare soil/rock, light biocrust, and dark biocrust. Other classes include vegetation, NPV and shadow. Shannon diversity (i.e., SCH_RS) was calculated with a moving window (0.5 × 0.5 m) using the Focal Diversity Python tool in ArcGIS Pro (version 2.9.2).

Data analyses

Effects of field-based soil cover and heterogeneity on plant diversity patterns

We used a four-step approach to evaluate relationships between field-based soil cover and SCH and plant diversity and community composition: (1) First, we performed preliminary data exploration with Pearson correlation and boosted regression tree analyses (BRT) to test for potential relationships among candidate soil predictor variables (Table 1) to inform model selection. (2), Then, we used linear mixed effects models to investigate relationships between soil predictor variables and variation in patch plant diversity. (3) Next, we examined evidence of possible mechanisms driving plant diversity responses to SCH using analyses to explore species sorting (i.e., indicator species analysis; Dufrêne & Legendre 1997), spatial turnover, and density-richness relationships. (4) Finally, we used permutational multivariate analysis of variance (PERMANOVA) to test whether patch soil cover and SCH structured plant community composition. All statistical analyses were conducted in R version 4.3.2 (R Core Team 2023). Alpha = 0.05 was used to determine significance level for all statistical analyses.

Correlation analysis and boosted regression tree data exploration

Before developing predictive models for plant diversity metrics, we explored relationships among variables. We first tested all variables for multicollinearity (Neter et al. 1996) by examining cross-correlations (Pearson correlation coefficients, r) between variables using the Hmisc package (Harrell & Harrell 2019). When the correlation coefficient between two soil predictor variables was $|r| \geq 0.65$ (Taylor 1990), one of the two variables was discarded prior to subsequent analyses. We then used boosted regression tree (BRT) analysis with forward stepwise multiple regression to identify influential soil predictor variables and eliminate non-significant predictor variables from models using the 'gbm.step' function in the gbm (Ridgeway 2013) and dismo packages (Hijmans et al. 2017) as in Elith & Leathwick (2017). Models were simplified using the 'gbm.simplify' function suggested by Elith and Leathwick (2017). Simplified BRT models for each analysis included the most influential moderators and ranked them according to their relative contributions (which are scaled to sum to 100% within each model—i.e., the predictor variable explains X % of the variation explained by the fitted BRT) to the explanation of variation in the response variable. Relative variable influences were derived as an average of variable influence in all trees in each BRT model (Friedman & Meulman 2003). Potential interactions between predictor variables in final BRT models were explored using the 'gbm.interaction' function (Elith & Leathwick 2017).

Mixed effects models: relationships between soil heterogeneity and plant diversity

Following the selection of influential candidate soil predictor variables to be retained in predictive models, we fit linear mixed models (LMEs) using the 'lmer' function in the *lme4* package (Bates et al. 2010) to test for relationships between plant Shannon diversity and soil predictor variables. We tested LMEs for assumptions of normality and heteroscedasticity using Shapiro–Wilk and Levene's tests (via the 'car' package; Fox et al. 2012) respectively. We used Akaiki's Information Criterion (AIC) adjusted for small sample size (AIC_c; Burnham & Anderson (2002)) to select final models for each response variable from the set of candidate LMEs developed. We used the '*r2*' function in the *performance* package (Lüdecke et al. 2021) to calculate marginal and conditional R^2 values associated with fixed and random effects in final models. For fixed effect variables that were found to be significant in the final model, we used univariate regression to explore relationships between plant H and influential predictor variables (e.g., SCH, percent dark biocrust cover).

Species sorting, spatial turnover, and density-richness relationships in patches with different levels of soil cover heterogeneity and biocrust cover

We tested for evidence of species sorting and among patches with low, medium, and high SCH and biocrust cover. We used indicator species analysis using the 'multipatt' function in the indicspecies package (De Caceres et al. 2016) to test for species affinities for a priori defined patch types (SCH: low = 1.75–2.50, medium = 2.51–3.25, high = 3.26–4.00; biocrust cover: low = > 25%, medium = < 25%-50%, high = > 50%-75%). Species were identified as being sorted when a significant indicator value among soil predictor levels was detected based on 999 randomizations. We also separately explored relationships between predictor variables and the cover of different plant functional groups (i.e., annual grasses, annual forbs, perennial grasses, perennial forbs) using univariate linear regression. Then, we used the 'beta.multi' function in the betapart package (Baselga et al. 2010) to calculate overall species turnover (Simpson's index for dissimilarity) and spatial turnover (Sørensen index for dissimilarity) for SCH patch types (Baselga 2010). To examine the potential relative importance of niche versus neutral processes in driving plant community Shannon diversity in patches with different levels of soil heterogeneity (Doncaster 2009), we also tested the strength of density-richness relationships among patches within low, medium, and high SCH.

PERMANOVA: relationships among plant community composition, soil cover, and soil cover heterogeneity

We separately tested for relationships among SCH, cover of soil cover classes, and plant community composition using PERMANOVA (permutation-based multivariate analysis of variance), with 9999 permutations and relativized Bray–Curtis dissimilarity (package 'vegan'; Oksanen & Blanchet 2016). To perform PERMANOVA model selection, we used the 'AICcPermanova' package (Corcoran & Corcoran 2023), which we used to generate all possible noncollinear models for our set of candidate predictor variables (Table 1), calculate associated AICc values, and select top candidate models.

Associations between UAS and field-based soil cover heterogeneity metrics

To validate how well UAS classifications represented individual soil cover types, we used linear regressions on the field patch point intercepts for (1) bare soil, (2) light biocrust, (3) dark biocrust and (4) total biocrust cover. Regressions were calculated individually for each 0.25 ha plot (n = 3), and each plot contained 8 subplots consisting of 100-point intercept data points each (Fig. 2). We tested relationships between the percent area of each class in a 0.5-m^2 quadrat compared to a fishnet grid of 100 points that roughly approximated the locations of the point intercept data (Fig. 2) and found strong relationships between the two (bare soil: $R^2 = 0.91$, light biocrust: $R^2 = 0.96$, dark biocrust: $R^2 = 0.86$, and total biocrust: $R^2 = 0.98$). We therefore used the 0.5-m^2 areal estimates of percent cover in further regression analyses.

Associations between UAS soil cover heterogeneity and plant diversity

We used linear regression to explore associations between UAS soil cover heterogeneity (SCH_RS) and field-based plant Shannon diversity at the patch level. Mean (SCH_RS_avg) and maximum (SCH_RS_max) values were extracted from the rasters based on polygons outlining the 0.5-m^2 soil quadrats.

Results

Plot characteristics: groundcover, climate, and livestock grazing

Average plant cover within study plots was 45.0 (stdev = 16.8%). Mean plant species richness was 3.60, stdev = 1.60 species (Sage A = 3.43, stdev = 0.49; Sage D = 3.13, stdev = 0.83; Sage E = 4.13, stdev = 1.73). Mean plant Shannon diversity was 2.4 (stdev = 0.90) (Sage A = 2.62, stdev = 0.65, Sage D = 2.61, stdev = 1.31, Sage E = 2.06, stdev = 0.49). Mean bare soil cover within plots was 23.6 ± 16.9%, light cyanobacterial biocrust cover was 24.2 ± 15.7%, and dark biocrust cover was 7.6 ± 8.9%. Overall, Sage_A had a high cover of bare soil and light cyanobacterial biocrust cover, whereas Sage_D and Sage_E had more mixed cover of bare soil, light cyanobacterial biocrust, and dark biocrust cover. Plant cover in Sage_A was typically dominated by perennial and annual grasses (especially *B. tectorum*), while Sage_D and Sage_E had higher cover of perennial grasses and some forbs. There was a substantial drought during the 2018 growing season. Precipitation in the 12 months leading up to our field survey in June 2018 was 58.9% lower (Fig. S1) and mean temperature was 1.4 °C higher (+ 11.2%) than the 30-year long-term averages during this time period (Fig. S1). Based on field estimations, qualitatively assessed grazing levels were variable in plots ranging from low to high.

Data exploration: relationships between measures of soil cover heterogeneity and plant diversity

Pearson correlation analyses showed that plant richness and plant Shannon diversity (H) were highly correlated ($r = 0.87$, $p < 0.001$; Fig. S2) and were similarly correlated to candidate predictor variables. As such, we made the decision to proceed with subsequent analyses only for plant diversity. Plant diversity was positively correlated with SCH ($r = 0.40$, $p = 0.011$; Fig. S2), and soil depth ($r = 0.49$, $p = 0.002$; Fig. S2), and marginally, with dark biocrust cover ($r = 0.41$, $p = 0.053$; Fig. S2). Boosted regression tree (BRT) data exploration showed that the candidate soil predictor variables with significant explanatory power in predicting plant diversity were SCH, dark biocrust cover, bare soil cover, and soil depth.

Predictive linear mixed effects models of herbaceous plant diversity

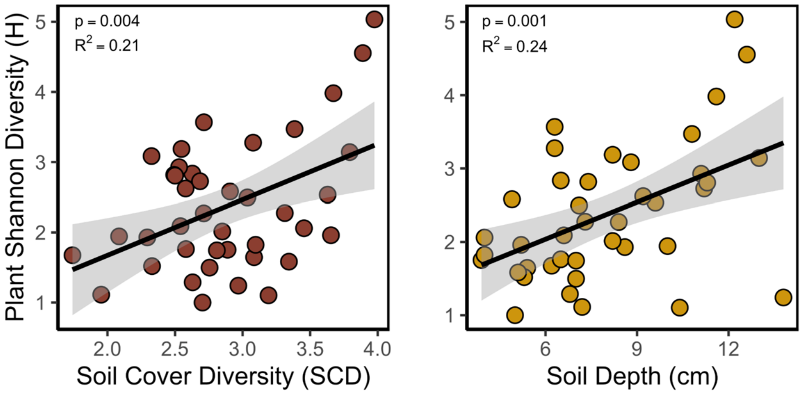
Using influential candidate soil predictor variables identified by correlation and BRT analyses, we generated predictive linear mixed effects models for plant Shannon diversity. The best model included SCH, percent dark biocrust cover, and their interaction as fixed effects. Soil depth and grazing were included as random effects. Plant diversity was positively associated with both SCH ($X^2 = 4.298$, $p = 0.038$; Table 2) and the interaction between SCH and percent dark biocrust cover ($X^2 = 6.610$, $p = 0.010$; Table 2). Univariate regression on significant variables showed that plant diversity increased with increasing SCH ($t = 2.68$, $p = 0.010$; Fig. 3) and soil depth ($t = 3.43$, $p = 0.001$; Fig. 3), and marginally, with dark biocrust cover ($t = 2.01$, $p = 0.052$; Fig. 3).

Table 2 Linear mixed effects (LME) model results for herbaceous plant Shannon diversity

LME and Wald Type II ChiSquare analysis of deviance test results showing significance in fixed effects. Soil depth (1|Soil_Depth) and (1|Grazing) were included as random effects

Predictor	Est	SE	*t*-value	LME				Wald Type II ChiSquare
				R^2m	R^2c	df	X^2	*P*-value
Plant Shannon Diversity								
(Intercept)	2.413	1.108	2.178	0.32	0.71			
Soil cover heterogeneity (SCH)	− 0.124	0.418	− 0.297			1	4.298	**0.038***
Dark biocrust cover (%)	− 0.242	0.102	− 2.382			1	0.735	0.391
SCH * Dark biocrust (%)	0.086	0.034	2.571			1	6.610	**0.010****

Fig. 3 Univariate relationships between plant Shannon diversity and soil variables included in the LME (soil cover heterogeneity (SCH), and soil depth (cm)



Species sorting, spatial turnover, and density-richness relationships

Indicator Species Analysis identified plant species associated with different soil patch types with respect to patch soil cover heterogeneity and biocrust cover. Perennial grasses *Elymus elymoides* (squirreltail) and *Achnatherum hymenoides* (Indian ricegrass) were found at greater abundance in patches with high SCH relative to other SCH patch types (IndVal = 0.632; $p = 0.005$ and IndVal = 0.237; $p = 0.050$ respectively). We also identified species as sorting with respect to levels of patch dark biocrust biocrust cover. *Elymus elymoides* (IndVal = 0.555, $p = 0.014$) and annual forb *Plantago patagonica* (wooly plantain; Indval = 0.365; $p = 0.043$) were associated with high biocrust cover, *Sclerocactus whipplei* (Whipple's fishhook cactus; Invdal = 0.474; $p = 0.098$) was marginally associated with medium biocrust patches, and invasive annual grass *Bromus tectorum* (cheatgrass) was associated with low biocrust patches (Indval = 0.739; $p = 0.029$).

Regression analyses between SCH variables and cover of plant functional groups showed that while patch total plant cover was negatively associated with total biocrust cover within patches overall ($r = -0.57$; $p < 0.001$; Fig. S2), this relationship was not consistent across plant functional types. In similarity to ISA results, annual grass cover decreased with increasing total biocrust cover ($p = 0.003$; Fig. S3a). The annual grass category was almost entirely composed of the invasive exotic grass species *B. tectorum*, indicating biocrust cover was negatively associated with *B. tectorum* cover at the patch scale. In contrast, we found a small but significant increase in annual forb cover with increasing total biocrust cover ($p = 0.034$; Fig. S3c). While we found evidence of species sorting by SCH levels and biocrust cover, analysis of species turnover showed communities in patches with high SCH (heterogeneous) did not differ significantly in their spatial turnover compared to medium or low SCH (homogeneous) patches (all $p > 0.05$, Table S2). Species rarefaction curves indicated high SCH patches accumulated more species over standardized densities than patches with lower heterogeneity (Fig. S4). Analysis of density-richness relationships among patches with low, medium, and high SCH showed that density-richness relationships were relatively weak, with no significant density-richness relationships among SCH patch types (all $p > 0.05$; Fig. S5).

PERMANOVA: plant community composition

The final PERMANOVA model included SCH, percent total biocrust cover, percent bare soil cover and their interactions (Table 3). Results showed that plant community composition varied marginally related to patch soil cover heterogeneity (SCH; $p = 0.059$), and significantly by percent bare soil ($p = 0.003$) and the interaction between SCH and bare soil cover ($p = 0.013$, Table 3).

Table 3 Relationships among SCH, soil cover and herbaceous plant community composition

Predictor variable	df	SS	R^2	Pseudo-*F*	*P* value
Soil cover heterogeneity (SCH)	1	0.369	0.046	2.126	***0.059***
Total biocrust cover (%)	1	0.244	0.031	1.404	0.204
Bare soil cover (%)	1	0.689	0.087	3.971	**0.003****
SCH × Total biocrust cover (%)	1	0.177	0.022	1.021	0.393
SCH × Bare soil cover (%)	1	0.516	0.065	2.971	**0.023***
Total biocrust × Bare soil cover (%)	1	0.129	0.016	1.633	0.170
SCH × Total biocrust × Bare soil cover (%)	1	0.129	0.016	0.746	0.577
Residuals	32	5.555	0.698		
Total	39	7.964	1.000		

Results for PERMANOVA analysis of relativized Bray–Curtis dissimilarities for herbaceous plant community structure in relation to soil cover heterogeneity (SCH), total biocrust cover (%), grazing level, and their interactions

df degrees of freedom; *SS* sum of squares, *Pseudo-F F* value by permutation

Bold face indicates statistical significance ($P < 0.05$); *P*-values are based on 9999 permutations (i.e., the lowest possible *P*-value is 0.0001). Significance codes: < 0.001 '****', < 0.01 '**', < 0.05 '*', < 0.1 '.'

UAS validation and classification results

Our comparison between field-based data measured within 0.5-m^2 quadrats to UAS estimates of percent cover yielded mixed results that varied considerably by 0.25 ha plot. Dark biocrust had the highest overall R^2 (0.50), ranging from 0.84–0.06 at the plot level (Fig. 4). Light biocrust ranged from $R^2 = 0.34$ to 0.14 but had no significant relationship across plots (Fig. 4). Bare soil had high correlations at one plot (Sage E, $R^2 = 0.81$), but weak correlations at two other plots (Fig. 4). Much of the error and variability observed was related to confusion between bare soil and light biocrust, and similarly between dark biocrust and shadows. While this quantitative comparison offers some estimation of the accuracy of our UAS SVM image classifications, it should be noted that geolocating the exact spots where field point intercept measurements were made on sub-centimeter imagery is challenging and slight positional differences between the two data sets can cause misalignment of validation data (Fig. 2). Given the ultra-high pixel resolution UAS imagery, visual comparison of classified UAS imagery vs. the UAS RGB orthoimages and field photographs (Fig. 2) provide additional subjective evidence of map quality; The classified maps produced for this project do well to represent the observed patterns of soil, biocrust and vegetation represented in the images (Fig. 5), despite the expression of error quantified using field methods at the patch scale (Fig. 4).

UAS distribution of soil cover classes and soil cover heterogeneity across plots

The classified images of the larger 50-m plots showed variation in the amount and distribution of vegetation, biocrusts, and soils. Sage A was dominated by

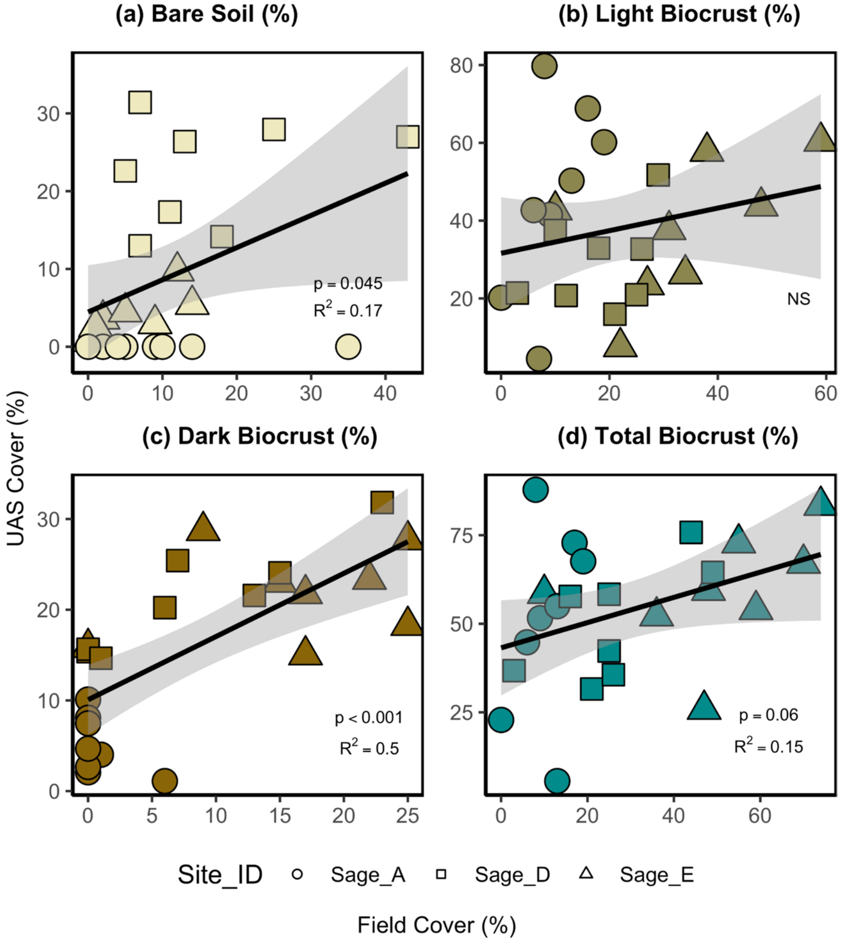


Fig. 4 Scatterplots showing the relationship between percent cover of field measured soil cover classes and percent cover of classified UAS imagery for 24, 0.5-m^2 quadrats measured across three study plots in Beef Basin, UT

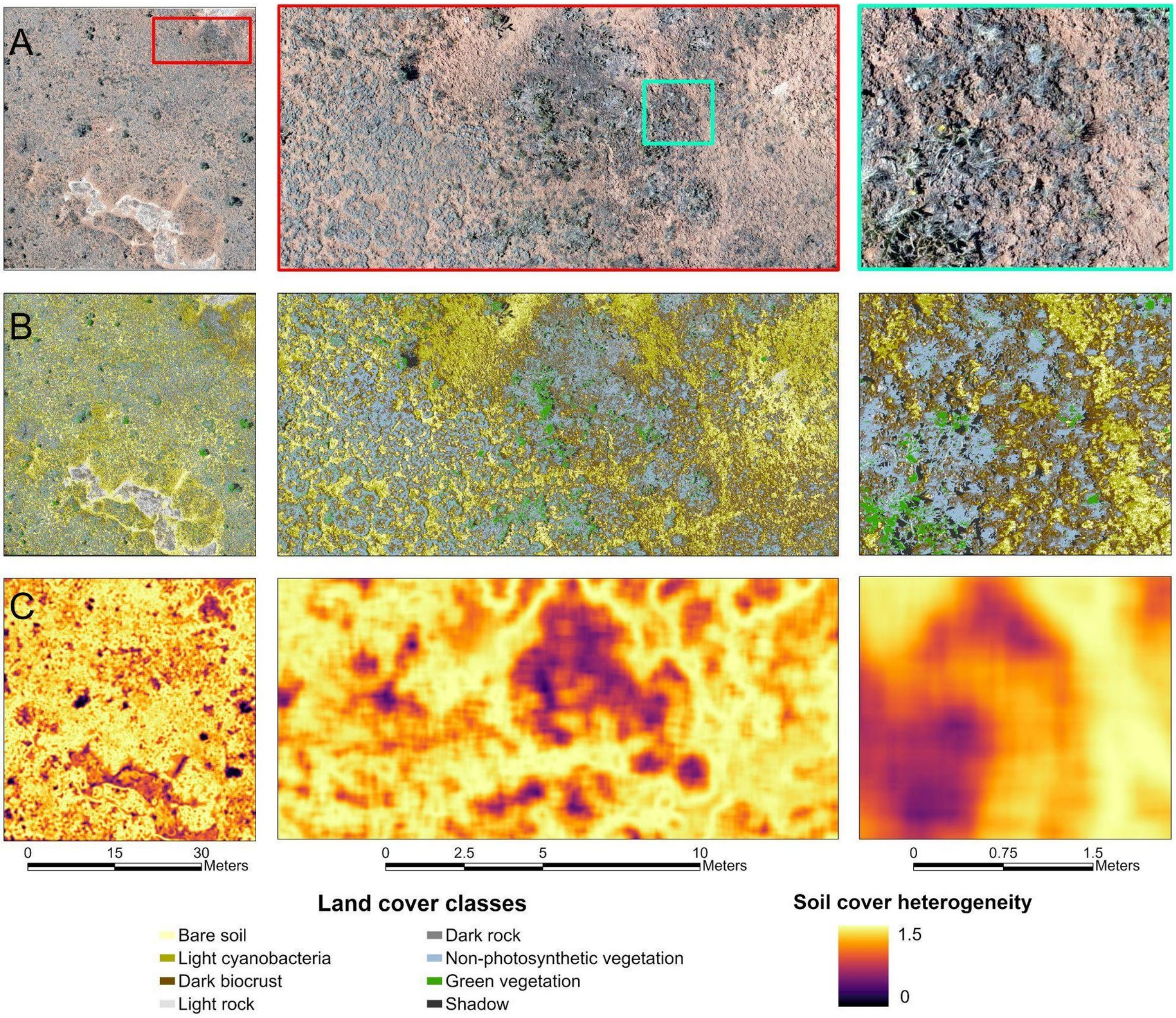


Fig. 5 Plot-scale map (row **A**) and zoomed details (1:66 and 1:17 respectively) of original high resolution (0.3 cm) RGB orthomosaic images, support vector machine (SVM) image classifications (row **B**) and remotely sensed soil cover heterogeneity (RS_SCH_RS) (row **C**). Red and blue boxes indicate the area of detail of the images to the right

non-photosynthetic vegetation (NPV; 60.3%) which was mostly in the form of senescent bunchgrasses, with 30.7% light biocrust, 4.21% dark biocrust and < 1% bare soil. Sage D had a more even mix of cover types with 19.6% NPV, 15.7% light biocrust, 15.9% dark biocrust and 19.2% bare soil. Sage E had the greatest total biocrust cover with 28.1% light biocrust, 18.0% dark biocrust, 16.4% NPV and 5.2% bare soil. Green vegetation represented a small proportion of cover in each plot and ranged from 3.7% (Sage A) to 11.3% (Sage E). Plot-level soil cover heterogeneity was highest at Sage D (mean SCH_RS = 1.14, stdev = 0.23) followed by Sage E (mean SCH_RS = 1.00, stdev = 0.25). Sage A had low average plot soil cover diversity (mean SCH_RS = 0.64, stdev = 0.26). SCH_RS varied spatially across individual plots, and visual comparison shows cross-site differences in spatial patterns, with considerable heterogeneity in Sage A and homogeneity in Sage E (Fig. 6).

Relationships between remotely sensed soil cover heterogeneity and ground-based plant diversity Plot-level SCH_RS patterns (where Sage D > Sage E > Sage A) did not align to observed patterns of field-based plant diversity (Sage A > Sage D > Sage E).

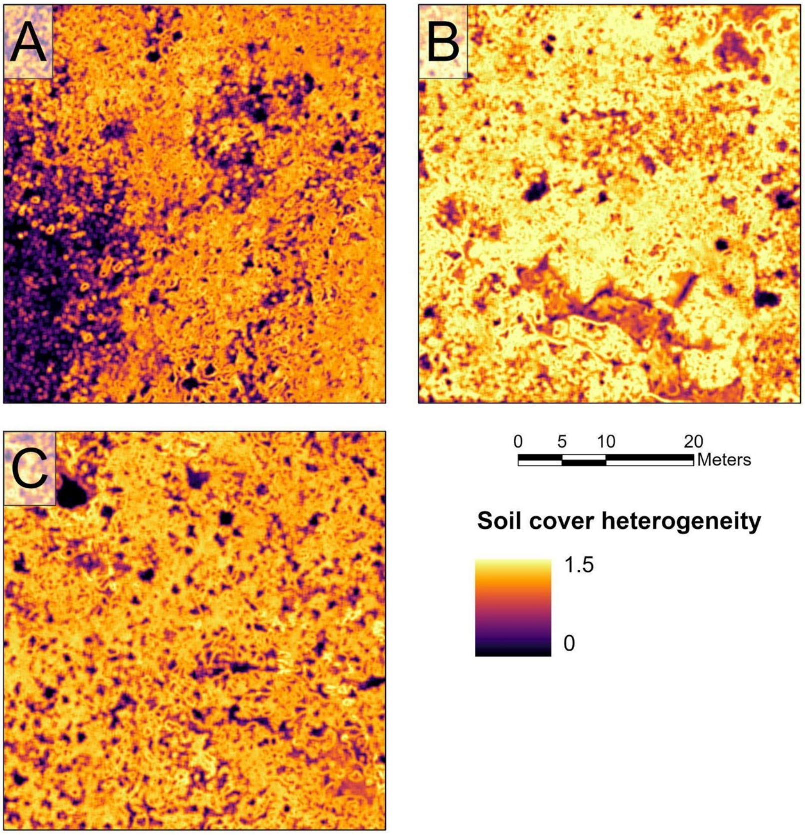


Fig. 6 Plot-scale SCH_RS maps of three sites, Sage A (**A**), Sage D (**B**) and Sage E (**C**) generated from support vector machine (SVM) classifications

Similarly, at the patch-level, linear regression showed no significant associations between average or maximum SCH_RS and plant Shannon diversity ($p > 0.05$). Though, within Sage D and Sage E plots, field-based plant diversity trended higher with higher maximum SCH_RS (Fig. S6).

Discussion

We used field-based soil and plant surveys and high-resolution UAS remote sensing to explore co-occurrence patterns between biocrust-associated soil cover heterogeneity (SCH) and local plant diversity in a cool-desert ecosystem in the Colorado Plateau Ecoregion, USA. Further, we tested whether remote sensing data could be used to calculate robust SCH metrics that could be used to extrapolate these patterns across larger landscapes. We found that (1) biocrust-associated SCH predicted local plant diversity and community composition patterns at the patch scale. Specifically, plant Shannon diversity increased with increasing SCH and dark biocrust cover, and SCH predicted plant community diversity patterns with evidence of species sorting into patches with different levels of SCH. (2) Second, we found that while the accuracy of UAS-mapped soil cover classes varied across sites due to variation in timing and quality of image collections, UAS are a promising data source for generating highly detailed, spatially explicit SCH metrics. These findings improve understanding of co-occurrence patterns between biocrusts, soil cover heterogeneity and plant diversity in drylands and highlight the potential of UAS to map and scale metrics of soil cover heterogeneity.

Soil cover heterogeneity and biocrust cover predicted plant diversity and community composition

Overall, field-based, biocrust-associated SCH was positively associated with plant diversity (H) at the patch scale. This finding aligns with results of past studies that have shown positive relationships between soil heterogeneity and plant alpha diversity patterns (e.g., Wijesinghe et al. 2005; Williams & Houseman 2014) and could have several possible explanations. First, differences in total plant density among patches could explain differing levels of plant diversity among patches. Community theory predicts a strong relationship between plant species richness and plant density and often suggests neutral-type assembly processes (a sampling effect) where stochastic colonization and extinction generate richness patterns that are largely dependent on total plant density (Hubbell 2005). However, we found no strong differences between density-richness relationships among patches with different levels of SCH (Fig. S5). Further, species rarefaction curves suggested that high SCH patches accumulated more species over standardized densities than patches with lower heterogeneity (Fig. S4). That more species accumulated in patches with greater soil surface heterogeneity (i.e., higher SCH) is consistent with theoretical predictions that plant community assembly is driven by niche type processes in harsh environments like drylands (Trexler et al. 2005; Chase 2010), and, here, may be mediated in part by soil cover heterogeneity. Since we found no evidence of density-dependent drivers of plant diversity among SCH patch types, a second possibility is that plant species diversity is higher in more heterogeneous patches because of differential species sorting which can generate differences in spatial turnover among patch types (Hutchinson 1957; Chase & Leibold 2009). Though there were no detectable differences in species turnover among SCH patch types (Table S2), we did find evidence of species sorting of indicator species into patches with different levels of SCH. This result, along with observed increases in local plant diversity in patches with higher SCH (Fig. 3), aligns with predictions that soil cover heterogeneity may increase plant diversity by promoting coexistence through niche differentiation. Though it is also possible that alternatively, plant diversity could also in part drive patterns of SCH.

Biocrust cover was also associated with plant diversity. Plant diversity increased with increasing dark biocrust cover (i.e., cover of biocrusts dominated by dark cyanobacteria, mosses, and/or lichens). This result is consistent with studies that have found positive correlations between biocrust cover and plant diversity (Kleiner & Harper 1977; Jeffries & Klopatek 1987; Luzuriaga et al. 2012; Scott & Morgan 2012) and may suggest that biocrusts support plant diversity by promoting increases and/or greater heterogeneity in soil resource availability in space and/or time (Concostrina-Zubiri et al. 2013), thereby promoting plant coexistence through niche differentiation. Species sorting into patches with low vs high biocrust cover observed in our study supports this assumption. For example, that perennial C3 grass species *Elymus elymoides* (squirreltail) and *Achnatherum hymenoides* (Indian ricegrass) showed greater abundance in patches with high dark biocrust cover could suggest affinity for recruitment and/or higher fitness of these species in biocrust microsites. Conversely, higher occurrence of invasive annual grass *Bromus tectorum* (cheatgrass) in low biocrust cover patches is consistent with the results of a global meta-analysis by Havrilla et al., (2019) found that biocrusts tend to inhibit recruitment of non-native plant species. Nonetheless, such species co-occurrence patterns could be associated with patch disturbance legacies (see Livestock grazing section below) or low sample size. Though the mechanisms underlying these patterns remain uncertain, results indicate that patterns of biocrust-associated soil cover heterogeneity can be used to predict plant diversity patterns.

UAS are a promising data source for generating highly detailed, spatially explicit soil cover heterogeneity metrics

We demonstrated that UAS-based land cover classifications can in some cases adequately capture spatial distribution of soil cover types at very high resolution, and maps of soil cover heterogeneity (i.e., remotely sensed soil cover heterogeneity; SCH_RS) generated from classified UAS imagery can provide a means to visualize and assess landscape-scale patterns. We observed considerably different patterns of SCH at the plot scale (Fig. 6), driven by the composition and distribution of land cover classes, including the abundance of vegetation and non-photosynthetic vegetation. The two plots (Sage D and Sage E) with an even mix of land cover types, low non-photosynthetic vegetation, and high proportion of dark biocrust, displayed highest SCH_RS associated with greater plant diversity. At these two plots, patch-level SCH_RS metrics generally corresponded with field-measured plant diversity (Fig. S6), suggesting that UAS data are useful for characterizing and modeling diversity at both the patch and the plot scales. However, in the remote sensing models the lowest plot and patch SCH was observed at Sage A, and these findings did not agree with the field-based measures. Validation of UAS-classified soil cover with field-measured point-intercept data showed low correlations of bare ground and dark crust in the Sage A plot, which contributed to a low estimate of SCH_RS and weak relationships to field-measured plant diversity.

The variability in the accuracy of the UAS classifications among plots made direct comparison to the patch- and plot-level plant diversity data challenging. Inconsistencies in modeled data arising from use of different UAS image sets flown at different locations, times and under different conditions can complicate landscape-scale studies. Even while employing standardized image collection protocols, variable environmental conditions like wind and ambient lighting can impact the quality and radiometric consistency of different image collections, impacting classification results and making cross-plot comparisons difficult. Problems with UAS data collections often do not become obvious until the data are processed in the days or weeks after field campaigns. These obstacles, and the need for potential redundancy in UAS and field collections, should be recognized when designing studies that seek to integrate field and UAS data collections that represent variability over landscape gradients.

Furthermore, the challenge of aligning sub-centimeter resolution UAS data with sub-plot scale field measurements is an issue vexing ecologists who are working to integrate the two (Buters et al. 2019; van Blerk et al. 2022). In our case, it was difficult to confidently locate the field-measured intercept points at an exact location on UAS maps that were meant to capture pixel-level soil cover heterogeneity. This type of positional error can be overcome with use of object-based image classification methods that group similar pixels into larger objects (as were applied in our previous study, see Havrilla et al. 2019). This approach may be desirable in UAS rangeland monitoring applications where soil cover heterogeneity is not of interest and where pixel-based classifications may introduce noise into vegetation cover classifications (Gillan et al. 2020), but in our case the soil and biocrust signals would be lost by grouping pixels into larger “objects.” Based on our experience attempting to characterize fine-scale patterns within a 0.5-m^2 quadrat from UAS imagery, we suggest collecting field-photographs at multiple elevations, angles and zooms of the plot and surrounding area during the data collection effort. High quality field photos can act as additional reference sources when needed (Fig. 2).

Despite these challenges, high resolution UAS images remain a promising source of data for capturing spatial patterns of soil surface microbial communities, and maps of biocrust types, abundance and distribution can provide insight into ecosystem function at local to landscape scales (Havrilla et al. 2019; Blanco-Sacristán et al. 2021; Kozar et al. 2024). It may be possible to further scale UAS-mapped biocrust observations using high- and moderate-resolution satellites through spectral unmixing (Riihimäki et al. 2019), opening additional opportunities to investigate biocrust-plant relationships across larger landscapes and environmental gradients. Recent research estimating biocrust fractional cover from moderate-resolution satellite imagery (Rodríguez-Caballero et al. 2014; Poitras et al. 2018; Enterkine et al. 2024) shows promise for quantifying the heterogeneity of biocrusts, vegetation and soils within pixels and over large landscapes. But unlike green vegetation that display distinctive spectral signatures in the visible and infrared wavelengths, dry biocrusts often display spectral responses similar to bare soil (Rozenstein and Adamowski 2017) and non-photosynthetic vegetation/plant litter, creating challenges for remote detection at any pixel resolution. Because of these challenges and because biocrust appearances can vary considerably in different environments and geographies, biocrust remote sensing remains an active research topic. Airborne hyperspectral imaging of biocrusts shows considerable promise for differentiating biocrusts from soils, especially when image collection campaigns are timed to exploit photosynthetic activity during and after precipitation (Rodríguez-Caballero et al. 2017).

Study limitations, future directions, and broader applications

*F*ield data from our study provides preliminary support for the hypothesis that biocrust-associated SCH is positively associated with plant alpha diversity and that patterns of SCH can be more broadly assessed through calculation of remotely sensed metrics of SCH. However, observed mismatches between

UAS-derived SCH metrics and field-based plant diversity in our study highlight challenges that remain in using this approach to assess these patch-level patterns at multiple scales. Considerations of these limitations allow us to identify future study directions and broader applications of our findings.

Interpreting soil cover heterogeneity-plant diversity relationships in the context of broader environmental and disturbance gradients

Investigating soil cover heterogeneity-plant diversity relationships in situ is challenging because soil heterogeneity can rarely be measured in the absence of other potentially confounding environmental and/or disturbance gradients in natural systems. Similarly, in our study, several environmental factors may have contributed to the observed patterns in local plant alpha diversity patterns across gradients of biocrust cover and SCH.

Livestock grazing—First, cattle grazing likely contributed to observed soil cover patterns through direct effects on both plant diversity and soil cover. In dryland landscapes, livestock grazing is often a geologically novel disturbance (Asner et al. 2004) that can decrease plant diversity (Hanke et al. 2014; Herrero-Jáuregui & Oesterheld 2018) and biocrust cover as a result of physical disturbance via trampling (Zaady et al. 2016). In some drylands, grazing can impose an ecological filter that screens out all but a few plant species and functional groups, constraining diversity (Temperton et al. 2004). As such, while we might have expected that we would consistently find the highest plant diversity in patches with lower grazing pressure, we found no significant relationships between patch grazing level and plant diversity or community composition. Alternatively, grazing may have indirectly contributed to increased SCH within patches by fragmenting late-successional dark biocrust patches into diverse mosaics containing different biocrust successional stages and bare soil. Such small-scale disturbances can increase soil heterogeneity and species coexistence (Questad & Foster 2008). However, given Concostrina-Zubiri et al. (2013) showed high grazing intensity negatively impacts biocrust-mediated soil cover heterogeneity, heavier grazing might presumably diminish these effects.

Soil depth—Soil depth also differed across patches and was positively associated with plant diversity as has been shown in past studies (e.g., Dornbush & Wilsey 2010). Since plant diversity was positively associated with both SCH and soil depth, we are unable to parse apart the effects of soil cover heterogeneity and soil depth individually. Soil depth can vary with geomorphic conditions and soil composition, which may also drive patterns of SCH. To explicitly disentangle the effects of biocrust-mediated SCH, soil depth, and grazing on local plant diversity, future studies should attempt to quantify these effects in the absence of differences in soil depth and grazing, or across planned gradients in these variables in situ.

Climatic variability and drought—This study took place during a single growing season in which the community experiences a significant drought. Drought acts as a primary abiotic filter on annual plant community assembly in drylands (Luzuriaga et al. 2012) and can strengthen the dominance niche-type processes in determining plant community assembly (e.g., Chase 2010). As such, future research should explore whether biocrust-plant diversity patterns (particularly in the annual plant community) shift depending on interannual variability in precipitation and/or temperature across time.

Exploring heterogeneity-diversity relationships across multiple spatial scales

Environmental heterogeneity-species diversity relationships can be highly dependent on the spatial scale at which plant species diversity is quantified (Tamme et al. 2010). For example, while heterogeneity-diversity relationships are thought to be more variable at smaller spatial scales, at large scales (e.g., landscape level), different vegetation communities may coexist, promoting large regional species pool size and resulting in more consistently positive heterogeneity-diversity relationships (Tamme et al. 2010). As such, future work should evaluate relationships among biocrust cover, soil cover heterogeneity and plant diversity patterns across multiple spatial scales. Advances in remote sensing of plant biodiversity, particularly at species (reviewed in Chavan & Kulkarni 2023) and functional (Ustin & Gammon 2010) levels, combined with emerging techniques to remotely sense biocrust-associated soil cover heterogeneity demonstrated here, could provide opportunities to map and analyze patterns between SCH and plant diversity across larger landscapes.

Broader applications in landscape ecology, management, and conservation

Results from our study also indicate that similar approaches could be used for other applications in landscape ecology, management, and conservation. Biocrusts are microcosms that can be used as a model system for understanding the contributions of biodiversity and spatial patterning for maintaining ecosystem multifunctionality (Bowker et al. 2014). The relationships and methods demonstrated in our study open new possibilities for observational studies and experiments that explore the role of biocrust spatial patterns in determining ecosystem processes across larger spatial scales. As UAS sensors and classification models improve, so will our ability to accurately discern spatial distribution of plants, soils and biocrusts patterns at high resolutions. Ultra-high resolution UAS remote sensing is opening avenues of study into soil–plant dynamics that are less reliant on traditional field methods, and that can be more consistently measured and scaled over landscapes. These UAS techniques have applications beyond assessing biocrusts function in drylands: for example, von Nonn et al., (2024) similarly mapped spatial distribution of soil properties in post-fire environments, where abundance and distribution of different colored soils, charred soils, vegetation, and rock/cobble mapped from UAS can be used to predict post-fire erosion and sedimentation (von Nonn et al. 2024). Likewise, our understanding of wind erosion and dust production in drylands (Zhang et al. 2021) might be improved through the estimation of soil surface heterogeneity and microtopography using UAS data. Finally, novel applications of UAS imagery for modeling species microhabitats has been a major new advancement in the landscape ecology literature (Habel et al. 2016; Schenone et al. 2021; 2022; Gerber et al. 2023) and researchers are using these fine-scale data to develop habitat covariates at scales that are relevant to animals and insects. Like plant diversity, biocrusts are known to influence insect diversity (Li et al. 2006), and SCH and biocrust maps could serve as habitat variables for understanding habitat relations across larger areas though improvements are still needed to match field and remote sensing observations.

Conclusions: soil cover heterogeneity associated with biocrusts shows promise to predict local plant diversity patterns

Results from this study demonstrate positive co-occurrence patterns between biocrust-mediated soil cover heterogeneity and plant diversity and offer provisional support for the hypothesis that biocrusts may play a role in supporting local plant diversity by increasing SCH and niche differentiation for plant taxa with diverse resource requirements. UASs are a promising data source for generating highly detailed, spatially explicit soil cover heterogeneity metrics and developing methods show potential for investigation of these patterns across larger landscapes as well as other related applications. In the next several decades, biocrusts are expected to experience significant declines and compositional shifts worldwide in response to global change (Ferrenberg et al. 2015; Reed et al. 2016; Rodriguez-Caballero et al. 2018). Consequently, drylands may experience increased soil habitat homogenization. Increasing our understanding of how biocrusts, by contributing to soil cover heterogeneity, may drive plant community diversity and structure thus has important implications for predicting how drylands will respond to global change and may have applications for conservation and restoration planning across dryland landscapes.

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Author contributions CAH and MLV devised and planned the study. CAH collected and led analysis of ground-based field data. MLV conducted remote sensing analysis. CAH and MLV wrote the first version of the manuscript and edited and contributed to the final version of the manuscript.

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Data availability All data used for analysis of relationships among ground cover survey data and plant diversity and community composition will be archived on the Dryad Data Repository (doi TBD). Raw UAS images, orthomosaics, point clouds and digital elevation models (DEM) collected and generated for this study are available to download from USGS Earth Explorer (https://earthexplorer.usgs.gov/). The images are tagged with the Project ID "USGS_UT_Canyonlands_NP", which can be entered in the search criteria tab in the API.

Declarations

Competing interests The authors declare no competing interests.

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