



The pervasive and multifaceted influence of biocrusts on water in the world's drylands

David J. Eldridge¹  | Sasha Reed² | Samantha K. Travers¹ | Matthew A. Bowker³  | Fernando T. Maestre^{4,5} | Jingyi Ding¹ | Caroline Havrilla⁶ | Emilio Rodriguez-Caballero⁷ | Nichole Barger⁸ | Bettina Weber^{9,10} | Anita Antoninka³ | Jayne Belnap² | Bala Chaudhary¹¹ | Akasha Faist¹² | Scott Ferrenberg¹³ | Elisabeth Huber-Sannwald¹⁴ | Oumarou Malam Issa¹⁵ | Yunge Zhao¹⁶

¹Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia

²U.S. Geological Survey, Southwest Biological Science Center, Moab, UT, USA

³School of Forestry, Northern Arizona University, Flagstaff, AZ, USA

⁴Departamento de Ecología, Universidad de Alicante, Alicante, Spain

⁵Instituto Multidisciplinar para el Estudio del Medio "Ramón Margalef", Universidad de Alicante, Alicante, Spain

⁶U.S. Geological Survey, Southwest Biological Science Center, Flagstaff, AZ, USA

⁷Centro de Investigación de Colecciones Científicas de la Universidad de Almería and Experimental de Zonas Áridas (EEZA), Consejo Superior de Investigaciones Científicas, Almería, Spain

⁸Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, CO, USA

⁹Multiphase Chemistry Department, Max Planck Institute for Chemistry, Mainz, Germany

¹⁰Institute of Plant Sciences, University of Graz, Graz, Austria

¹¹Department of Environmental Science and Studies, DePaul University, Chicago, IL, USA

¹²Department of Animal and Range Sciences, New Mexico State University, Las Cruces, NM, USA

¹³Department of Biology, New Mexico State University, Las Cruces, NM, USA

¹⁴Division of Environmental Sciences, Instituto Potosino de Investigación Científica y Tecnológica, San Luis Potosí, SLP, Mexico

¹⁵UMR 242 (IRD, SU, CNRS, INRA, USPC, UPEC), IRD France-Nord, Bondy Cedex, France

¹⁶Institute of Soil and Water Conservation, Northwest A & F University, Yangling, Shaanxi, China

Correspondence

David J. Eldridge, Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia.
Email: d.eldridge@unsw.edu.au

Funding information

H2020 European Research Council, Grant/Award Number: 647038; U.S. National Science Foundation, Grant/Award Number: DEB-1638966 and DEB-1844531; US Strategic Environmental Research and Development Program, Grant/Award Number: RC18-1322; U.S. Department of Energy, Grant/Award Number: DESC-0008168; Generalitat Valenciana, Grant/Award Number: CIDEGENT/2018/041; Paul Crutzen Nobel Laureate Fellowship; Consejo Nacional de Ciencia y Tecnología, Grant/Award Number: 251388 B; Holsworth Wildlife Research Endowment

Abstract

The capture and use of water are critically important in drylands, which collectively constitute Earth's largest biome. Drylands will likely experience lower and more unreliable rainfall as climatic conditions change over the next century. Dryland soils support a rich community of microphytic organisms (biocrusts), which are critically important because they regulate the delivery and retention of water. Yet despite their hydrological significance, a global synthesis of their effects on hydrology is lacking. We synthesized 2,997 observations from 109 publications to explore how biocrusts affected five hydrological processes (times to ponding and runoff, early [sorptivity] and final [infiltration] stages of water flow into soil, and the rate or volume of runoff) and two hydrological outcomes (moisture storage, sediment production). We found that increasing biocrust cover reduced the time for water to pond on the surface (−40%) and commence runoff (−33%), and reduced infiltration (−34%) and sediment production (−68%). Greater biocrust cover had no significant effect on sorptivity

Ecological Society of Australia; China
Scholarship Council, Grant/Award Number:
201706040073; US Geological Survey;
DePaul University; Max Planck Society

or runoff rate/amount, but increased moisture storage (+14%). Infiltration declined most (−56%) at fine scales, and moisture storage was greatest (+36%) at large scales. Effects of biocrust type (cyanobacteria, lichen, moss, mixed), soil texture (sand, loam, clay), and climatic zone (arid, semiarid, dry subhumid) were nuanced. Our synthesis provides novel insights into the magnitude, processes, and contexts of biocrust effects in drylands. This information is critical to improve our capacity to manage dwindling dryland water supplies as Earth becomes hotter and drier.

KEYWORDS

biological soil crust, bryophyte, cryptogam, cyanobacteria, hydrological cycle, infiltration, lichen, sediment production, soil hydrology, soil moisture

1 | INTRODUCTION

Drylands (hyperarid, arid, semiarid, and dry subhumid environments; Huang, Yu, Dai, Wei, & Kang, 2017) represent our planet's largest terrestrial biome, covering over 45% of Earth's terrestrial surface and supporting about 40% of the world's population, many of whom rely heavily on primary production for their livelihoods (Cherlet et al., 2018; Millennium Ecosystem Assessment, 2005; Právělie, 2016). Current global climate predictions suggest that drylands will receive less rainfall, and experience higher temperatures, more severe droughts, and more frequent extreme events (IPCC, 2018). Changes in the rainfall regime of drylands are critical, as we know that water availability sustains dryland biota and regulates fundamental processes such as net primary productivity, decomposition and nutrient mineralization in these ecosystems (Leigh, Sheldon, Kingsford, & Arthington, 2010; Loik, Breshears, Lauenroth, & Belnap, 2004; Neumann et al., 2015; Sloat et al., 2018; Wang, Manzoni, Ravi, Riveros-Iregui, & Caylor, 2015). However, for drylands, our understanding of the factors that regulate biological access to soil water remains far from complete.

Recent syntheses of dryland ecosystems emphasize the hierarchy of processes and functions operating at different spatial scales and levels of connectivity (HilleRisLambers, Rietkerk, van den Bosch, Prins, & de Kroon, 2001; Ludwig, Wilcox, Breshears, Tongway, & Imeson, 2005). This heterogeneity has important implications for how water is moved and stored in drylands. Conceptually, dryland systems comprise two markedly different compartments or patch types, which either transfer (runoff zones) or accumulate (fertile patches) resources (Ludwig et al., 2005). Water is the means by which resources are transferred among patches, resulting in tightly coupled hydrological networks, with the effects at higher spatial scales cascading through to smaller spatial scales and vice versa. Vital, but often ignored components of these resource transfer zones are biocrusts, a rich assemblage of bryophytes, lichens, cyanobacteria and associated microscopic organisms such as bacteria, fungi, and archaea that occupy the uppermost layers of dryland soils worldwide (Weber, Büdel, & Belnap, 2016).

Biocrusts are critically important in drylands because they mediate key processes such as soil stabilization, and provide fundamental supporting, provisioning, and regulating services such as climate amelioration, nitrogen fixation, and carbon sequestration (Weber et al., 2016). One of the most important roles of biocrusts is their effect on water quality and delivery, the two ecosystem services associated with the hydrological cycle that sustain human populations and ensure environmental well-being. Biocrusts can moderate surface flows by partitioning rainfall between infiltration and runoff, regulate the horizontal and vertical fluxes of water, and reduce water erosion (Belnap & Lange, 2003; Weber et al., 2016). However, they are extremely vulnerable to human-induced disturbances and global changes (Dunkerley, 2010), which reduce their capacity to regulate hydrological functions across drylands. Despite the extensive body of literature on biocrusts (Weber et al., 2016), we still have a poor understanding of how they influence the hydrological cycle in drylands globally, particularly across variable environmental, climatic, and land use contexts (Whitford, 2002). The absence of a comprehensive synthesis of biocrust effects on hydrological processes complicates efforts to improve ecohydrological models to predict the fate of water, and to optimize water management in drylands (Chen et al., 2019; Shachak, Pickett, Boeken, & Zaady, 1999). The lack of synthesized information also limits our ability to develop best practices for managing biocrusts in order to optimize water management in drylands (Shachak et al., 1999). Such a synthesis is critical because Earth faces an increasing frequency and intensity of droughts and more unpredictable, extreme climates (Wang et al., 2015).

In this study, we report on a comprehensive global synthesis of the literature to date, of how biocrusts affect soil hydrology in drylands, where biocrusts are most strongly developed (Weber et al., 2016), and where any effects on hydrology are likely to have large impacts on both human livelihoods and natural ecosystems given the scarcity of water in these systems. We focused on seven key hydrological components; five hydrological processes (time to ponding, time to runoff, rate or volume of runoff [hereafter "run-off"], sorptivity, infiltration) and two hydrological outcomes (sediment production, soil moisture storage; Table 1; Appendix S1). The biocrust literature suggests that hydrological effects *sensu lato* are

TABLE 1 Description of the seven hydrological processes and outcomes, and the number of contrasts (*n*) used in the analyses

Processes and outcomes	Description	<i>n</i>
Time to ponding	Time taken for water to commence ponding on the surface after the commencement of rainfall	73
Time to runoff	Time from the commencement of rainfall to the first appearance of runoff	27
Sorptivity	The initial rapid stage of infiltration, occurring when the soil is initially dry and water flow is dominated by the soil's capillarity properties	135
Infiltration	Final or steady-state infiltration is the latter phase of infiltration and occurs once the flow rate is constant and gravitational forces are predominant	700
Runoff	Water that leaves the soil surface by overland flow	515
Soil moisture	A gravimetric or volumetric measure of the amount of moisture (soil moisture) stored in the soil	764
Sediment production	Sediment flux arising from natural or experimental runoff studies	382

likely context dependent (Chamizo, Belnap, Eldridge, Cantón, & Issa, 2016), so our hypotheses relate to hydrological effects of biocrusts under different environmental contexts. First, we expected that any biocrust effects would be regionally variable (e.g., arid cf. dry subhumid) due to differences in landforms, soil, and rainfall, and therefore runoff–runon relationships (Ludwig et al., 2005). Second, biocrust effects should vary with differences in broad soil textural classes (e.g., sand cf. clay), because texture determines the hydraulic conductivity of the underlying substrate (George et al., 2003), as well as soil erodibility, and, therefore, detachment (Cantón et al., 2011). Third, differences in biocrust composition (e.g., moss-, lichen-, cyanobacteria-dominated, or mixed) will influence the hydrological response by creating surfaces of varying permeabilities, or gradients in surface friction, and a patchwork of microsites with different levels of detention (Bowker, Eldridge, Val, & Soliveres, 2013; Eldridge et al., 2010; Faist, Herrick, Belnap, Van Zee, & Barger, 2017; Rodríguez-Caballero, Cantón, Chamizo, Afana, & Solé-Benet, 2012) which could alter runoff. Fourth, we expected the scale of measurement to influence the hydrological outcomes of rainfall because small-scale studies would lack features and processes such as patches of vegetation, surface roughness imposed by vascular plants, or channelized flow that would only influence runoff at larger spatial scales (Yair, Lavee, Bryan, & Adar, 1980). Finally, the level of surface disturbance would be expected to influence the degree to which biocrusts alter hydrological functions by altering the density and size of depressions that capture sediment, altering soil stability, or simply by destroying the protective biocrust surfaces.

2 | MATERIALS AND METHODS

2.1 | Scope of the database building

We systematically searched the scientific literature to identify quantitative evidence of the effects of biocrusts on different hydrological

functions. We searched the ISI Web of Science database (www.webofknowledge.com) for records prior to May 2020 and screened the information according to PRISMA guidelines (Figure S2.1 in Appendix S2) restricting our search to the keywords “CRUST*” or “BIOLOGICAL SOIL CRUST*” or “BIOCRUST*” or “CRYPTOGAM*” and “WATER FLOW” or “INFILTRATION” or “HYDRO*” or “SORPTIVITY” or “MOISTURE” or “EROSION.” We also checked records from the reference lists of the two most comprehensive biocrust syntheses conducted to date (Belnap & Lange, 2003; Weber et al., 2016) to test the extent at which our keywords captured critical biocrust hydrology literature. Suitable records were required to meet the following requirements for inclusion in our study: (a) restricted to terrestrial systems in drylands, in other words, where the aridity index (precipitation/potential evapotranspiration [P/PET]) was <0.65; (b) contained quantitative data on at least one of the seven hydrological measures; and (c) included data for at least two different levels of biocrust cover (see below). Sources that contained multiple data, for example a different response type or location, were considered separately (final list in Appendix S3).

For each study, we extracted data on the effects of biocrusts on five hydrological processes as follows: (a) time taken for water to pond on the surface (time to ponding); or (b) to commence runoff (time to runoff); (c) sorptivity (the early stage of infiltration; rate or volume); (d) steady-state infiltration (the latter stage of infiltration; hereafter “infiltration”; rate or volume); (e) runoff (rate or volume); and two hydrological outcomes: (f) soil moisture and (g) sediment production (Table 1). The sorptivity phase of hydrology is when water enters the soil in response to gradients in water potential influenced by soil dryness and pore structure, whereas infiltration is the latter stage when infiltration has stabilized and is regulated largely by hydraulic conductivity. Data presented in figures from published articles were extracted with ImageJ (Schneider, Rasband, & Eliceiri, 2012). For each study we also extracted data on location (e.g., country, latitude, longitude) and values for a range of moderators (see below). We consider both hydrological processes (time to

ponding and runoff, runoff, sorptivity, and infiltration) and hydrological outcomes (soil moisture storage, sediment production) associated with increasing cover of biocrusts.

2.2 | Calculating effect size

To determine the effects of biocrusts on hydrological processes and outcomes, we used the log response ratio $\ln RR = \ln(X_{\text{Higher}}/X_{\text{Lower}})$ as our measure of effect size (Hedges, Gurevitch, & Curtis, 1999), where X_{Lower} is the value of the response variable for the lower value of biocrust cover (detailed below), and X_{Higher} is the value for the response variable for the higher biocrusted comparison. Using this approach, negative values of the $\ln RR$ represent situations where hydrological processes and outcomes declined with increasing level of biocrust cover. Many studies reported a hydrological response from plots spanning a large range of biocrust cover values (e.g., 25 plots ranging in cover from 1% to 84% cover; Eldridge, Tozer, & Slangen, 1997). In this example with 25 plots, there are potentially 300 combinations of any two levels of biocrust cover. In the interest of parsimony, therefore, we assigned all records of biocrust cover to four cover classes as follows: bare ($\leq 10\%$ cover), low (10.1%–25%), moderate (25.1%–50%), and high ($> 50\%$ cover) and averaged the value of any response variable (and calculated an appropriate standard deviation) for that class to arrive at four values. In the situation described above, this gave us three values of $\ln RR$ where our values for low, medium, and high biocrust cover were compared with the bare (defined a priori as $< 10\%$ cover). We also calculated the $\ln RR$ for the following three additional contrasts: low compared with medium cover, low compared with high cover, and medium compared with high cover. Therefore, rather than comparing bare to either low, medium, or high, we always compare a lower level of cover with a higher level of cover to examine how a relatively greater level of cover (e.g., medium to high, or low to medium) will affect hydrological processes and outcomes. This allowed us to increase the size of our dataset, obtain more statistical power, and gave us a measure of the effectiveness of increasing biocrust cover on a particular hydrological process/outcome. For sediment production, we repeated the analysis where we used all contrasts ($n = 783$) with a restricted analysis where we compared crusted ($> 10\%$ biocrusts cover) with only bare soils ($\leq 10\%$ biocrusts cover; $n = 382$).

2.3 | Within study variance, meta-regression models, and moderator selection

To conduct meta-analyses weighted by within-study variance (Nakagawa & Santos, 2012), we collected data on the standard deviation (or standard error) and the number of replicates in our dataset. From these data we calculated the variance (standard deviation). If a study did not report a measure of variance (39% of cases), we used imputation to calculate missing variances using the relationship between mean and variance, expressed on a log–log scale (Taylor's

law; Nakagawa, 2015). Our ability to predict missing variances was high ($R^2 = .79$; further details in Appendix S4).

We used the intercept model (i.e., meta-analysis) and meta-regression with the R package metafor Vers. 1.9-8 (Viechtbauer, 2010). The intercept model uses a pure random effects model to estimate the overall log response ratio for the effect of biocrust on hydrological function, with individual effect sizes weighted by within-study variance and residual between-study variance as a random-effect (further details in Appendix S4). Three random factors were included in our null models: (a) a unique ID for each reference; (b) the order of the data within the data file; and (c) a measure of the difference in biocrust cover between any two contrasts. To calculate this measure of differences, we used the relative interaction intensity (Armas, Ordiales, & Pugnaire, 2004) of biocrust cover (i.e., higher cover – lower cover)/(higher cover + lower cover), which relativizes the effect of absolute values of changes in cover on our hydrological components, allowing, for example, a 10% change in cover from 0% to 10% to be weighted more heavily than a 10% change from 90% to 100%.

To control for the potential influence of shared controls, we included a coded group used to identify shared controls (Nakagawa & Santos, 2012). We ran separate intercept models for each of the seven hydrological components mentioned above because we were interested in examining the causes of variation within each component (sensu Nakagawa, Noble, Senior, & Lagisz, 2017). This is similar to meta-regression with categorical moderators (also known as Subgroup Analysis; Nakagawa et al., 2017; Nakagawa & Santos, 2012), allowing us to obtain heterogeneity statistics such as I^2 for each subset, and providing valuable information on how the overall response of hydrological function might vary across different components of hydrology. We used the modified I^2 to access the total level of heterogeneity among effect sizes. This modified I^2 indicates the percentage variance in effect size explained by each random factor (Nakagawa & Santos, 2012).

Because our meta-analysis (intercept) models had high levels of heterogeneity ($I^2 > 0.95$), we used a range of moderators (syn. fixed effects) with separate meta-regression models for each of the seven hydrological components, which allowed us to test our five predictions. For each component, we ran separate meta-regression models for each moderator (aridity, texture, biocrust type, scale, disturbance) as fixed effects, and the three random effects described above.

The five moderators (Table S5.3 in Appendix S5) were as follows: (a) Aridity was derived for each location using the CGIAR-CSI Global-Aridity and Global-PET Database (<http://www.cgiar-csi.org>; Zomer, Trabucco, Bossio, & Verchot, 2008). We calculated aridity as (a) 1 minus P/PET so that higher values of aridity corresponded to greater dryness. (b) Soil texture data (sand, loam, clay) were obtained from each paper; when data were missing, we contacted individual authors or used the Harmonized World Soil Database (6% of cases; Fischer et al., 2008) to derive a value. (c) Biocrust type was classified as cyanobacteria-, lichen-, moss-dominated, or mixed. This characterization was based on the predominant type

described by the author. Mixed biocrusts were generally those with either a mixture of cyanobacteria and lichens (40% of the mixed records) or mosses and lichens (35% of mixed records). For large, landscape-level studies, biocrust type was defined as mixed unless an author indicated that the entire site was dominated by one biocrust type only. (d) We calculated a continuous value for study scale by calculating the total area (m^2) over which hydrological function was assessed (e.g., a 1 m^2 rainfall simulation plot). This continuous scale was then divided into three classes: fine ($<0.05 \text{ m}^2$, generally Petri dish or small rainfall simulator, medium ($0.05\text{--}10 \text{ m}^2$; large rainfall simulators), and large ($>10 \text{ m}^2$, instrumented watersheds). The classes corresponded broadly to studies using infiltrometers (fine), small rainfall simulators (medium), and gauged catchments (large), and thus followed breaks in the data. (e) The level of disturbance (intact, reconstructed, disturbed) was obtained from individual publications. A comparison was deemed to be disturbed if one of the contrasts (control or treatment) was physically disturbed. The reconstructed category applied to studies where soil collected from the field had been used to regrow artificial biocrusts in the field or laboratory (e.g., Xiao, Wang, Zhao, & Shao, 2011). In addition, we recorded the depth of soil from which measurements of soil moisture were made in order to test whether biocrust effects on soil moisture declined with depth.

We created a covariance matrix to account for effect sizes with shared controls. We used the order of the data and the identity of the study as random effects in our models. True intercepts and standard errors were calculated for each level of ecosystem property so that results reflected true means rather than a comparison with a reference group. The significance of the estimated effect

size was examined with a t test on whether estimated effect size differed significantly from zero at $p < .05$. We calculated the variance accounted for by moderators as marginal R^2 (sensu Nakagawa & Schielzeth, 2013). Finally we used the package “segmented” (Muggeo & Muggeo, 2017) in R to examine whether the effects of increasing biocrust cover on lnRR soil moisture differed with three soil depths selected a priori 0–2, 2–5, and $>5 \text{ cm}$.

Publication bias was assessed using (a) funnel plots; (b) Egger regression; and (c) trim-and-fill analyses, which test for funnel asymmetry using Egger regression (Nakagawa & Santos, 2012) and the null hypothesis of no missing data (see Table S4.2 and Figure S4.2 in Appendix S4).

3 | RESULTS

Our literature search yielded 1014 references from which we identified 109 publications containing empirical data (see model results in Table S4.1 in Appendix S4). From these publications we extracted 2,997 contrasts of an effect of biocrusts on the seven hydrological variables from five continents (Asia, Europe, Australia, North America, Africa; Figure 1). Most data reported information on some form of water flow through the soil (infiltration, sorptivity; 28%; $n = 835$ contrasts) followed by moisture storage (26%; $n = 764$), sediment production (26%; $n = 783$), and runoff (17%; $n = 515$). Most studies (65%) were from semiarid areas (Figure 2a) or from sandy or loamy soils (85%; Figure 2b). Studies were relatively evenly distributed among the four biocrust types (Figure 2c). Ninety-one percent of studies were conducted at the fine ($<0.05 \text{ m}^2$) or medium

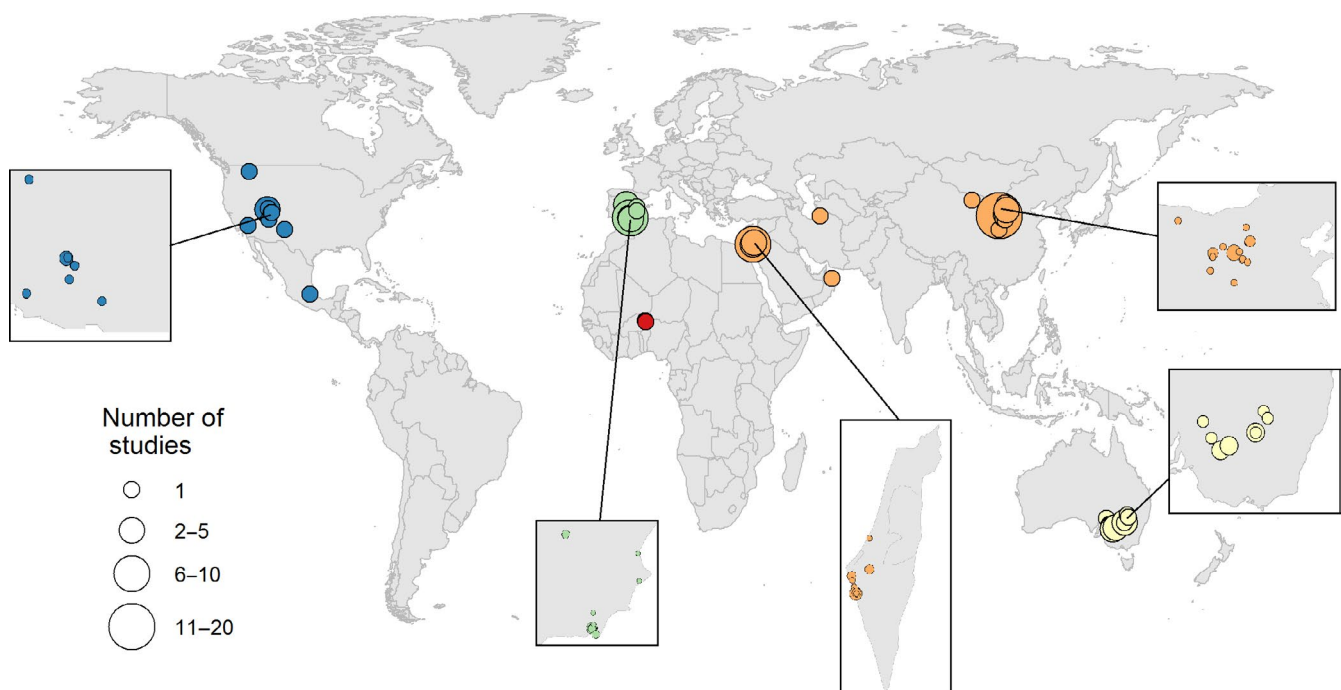


FIGURE 1 Map of the global distribution of sites used in the meta-analysis. Circle size represents the number of studies from each region. Inset maps show more site details for the main hotspots of biocrusts hydrological research

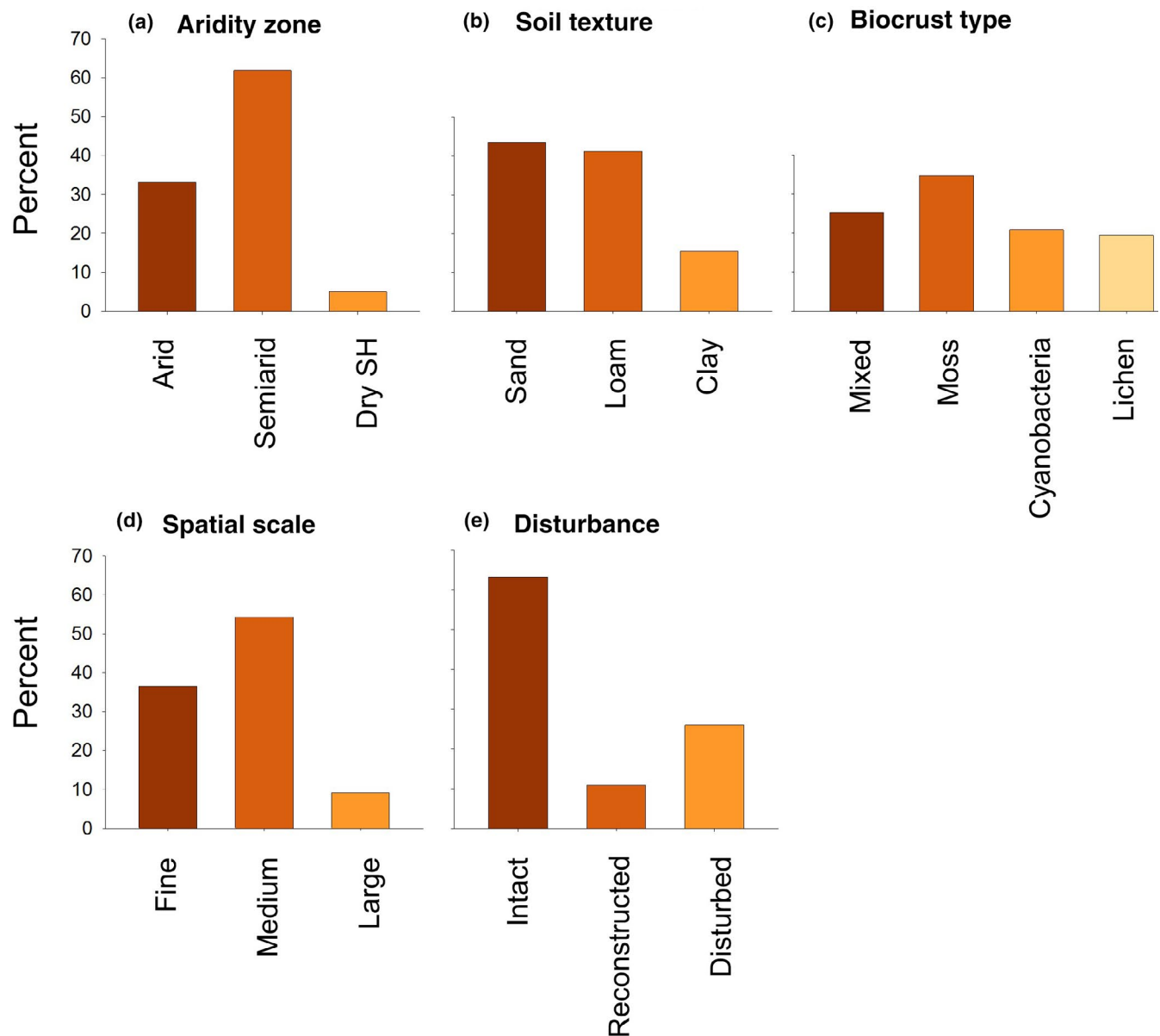


FIGURE 2 Percentage of records by (a) aridity zone, (b) soil texture, (c) biocrust type, (d) spatial scale and (e) disturbance. SH, subhumid

(0.05–10 m²) spatial scales (Figure 2d) and 63% were conducted on intact surfaces (Figure 2e).

Overall, with every 30% increase in biocrust cover, water ponded earlier (−40%), and runoff commenced earlier (−33%; Table S4.1). Infiltration (−34%) and sorptivity (−8%, but non-significant) declined as biocrust cover increased by 41% and 54%, respectively (Figure 3; Table S4.1 in Appendix S4). Sediment production declined (−68%), but soil moisture increased (+14%), as biocrust cover increased. Despite the general suppressive effects of biocrusts on infiltration, we found a non-significant increase in runoff rate/amount (+13%), which is consistent with the expectation of greater runoff with less infiltration. When we examined those studies reporting both infiltration and runoff individually ($n = 7$), we found that significant increases in infiltration were associated with declines in runoff (-1.60 ± 0.78 ; mean slope

of the runoff–infiltration relationship \pm 95% CI; Figure S6.3 in Appendix S6). Furthermore, despite lower infiltration, the uppermost (<0.5 cm) soil surface stored 60% more water than depths of 2–50 cm (Figure 4).

3.1 | Moderators of hydrological processes and outcomes

Increasing biocrust cover was associated with a 66% earlier commencement of ponding in arid areas, and 68% and 21% earlier commencement of runoff in arid and semiarid areas, respectively. Runoff did not vary significantly across different aridity zones, but infiltration was lower in semiarid (−33%) and arid (−39%) areas (Figure 5). The suppressive effect of increasing biocrust cover on sediment production

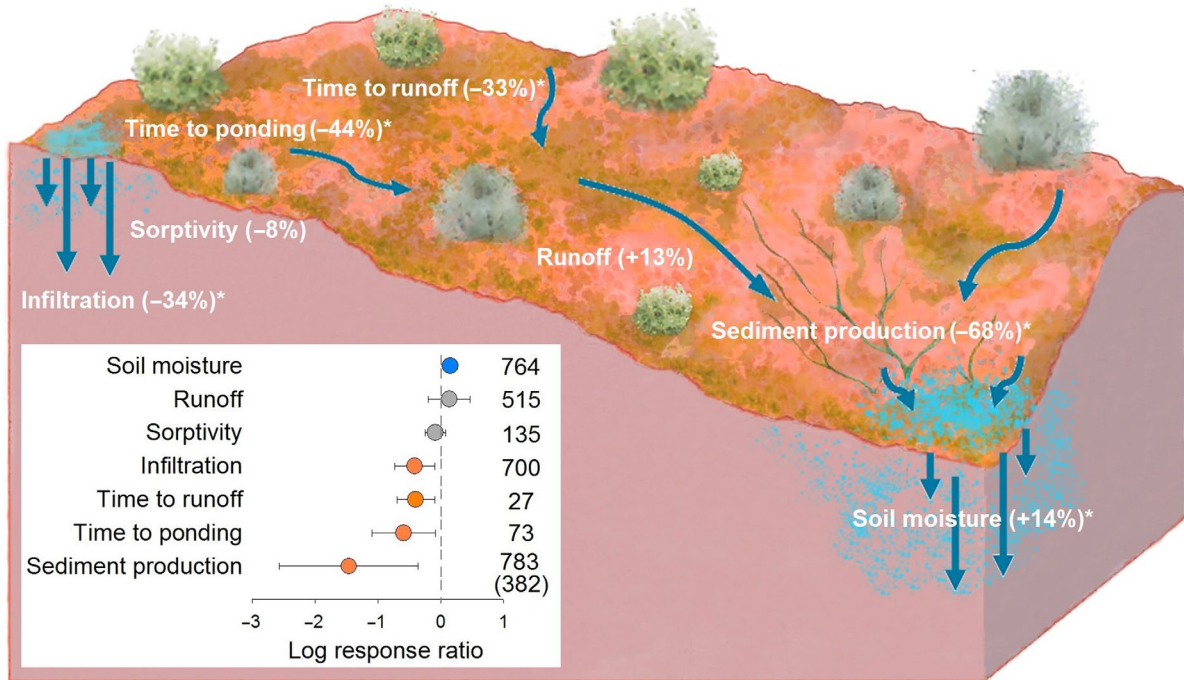


FIGURE 3 Schematic diagram of a dryland landscape showing the main processes and outcomes of water movement, soil moisture and sediment production and the overall percentage change resulting from greater biocrust cover. Asterisks indicate a significant ($p < .05$) effect increasing biocrust cover. Inset diagram shows the mean value of the log response ratio ($\pm 95\%$ CI) and the number of contrasts used in the analyses of each hydrological process or outcome. For sediment production, $n = 783$ for all contrasts, and $n = 382$ for the analysis restricted to bare ($<10\%$ cover) contrasts only (see text for details)

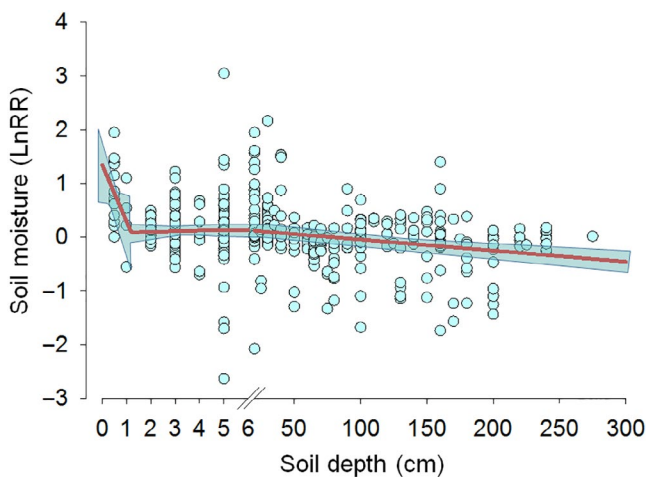


FIGURE 4 Changes in the log response ratio (LnRR) of soil moisture in relation to changing soil depth. The segmented regression analysis indicated three models, with a significant decline in soil moisture from 0.5-1 cm ($p = .045$), but no differences from 1 to 5 cm and 5 to 300 cm depths

was strongest in semiarid (-71%) areas. Despite the overall suppression of infiltration, increasing biocrust cover was also associated with 18% greater soil moisture in semiarid areas (Figure 5).

The effects of biocrusts on hydrological processes and outcomes also varied markedly with differences in soil textural classes. Increasing biocrust cover was associated with 17% and 13% greater

soil moisture, on loams and sands, respectively (Figure 5). On sandy soils, runoff increased ($+38\%$), but time to ponding (-52%), time to runoff (-47%) and infiltration (-49%) all declined with increasing biocrust cover (Figure 5), and the effects of increasing biocrust cover most strongly suppressed sediment production on loamy soils (-85% ; Figure 5).

We detected several effects of biocrust type on hydrological processes and outcomes. For example, sediment production was reduced mostly on mixed (-82%) or lichen (-78%) biocrusts (Figure 5), and the time to runoff declined with increasing cover of mixed (-34%) or cyanobacterial (-39%) biocrusts. The positive influence of biocrusts on soil moisture was most apparent beneath cyanobacterial biocrusts ($+23\%$), and increases in the cover of all biocrust types, other than lichens, reduced infiltration (by -31% to -46%), but there were no effects of biocrust type on sorptivity or runoff (Figure 5).

Infiltration declined with increasing biocrust cover at fine (-56%) and large (-49%) spatial scales. For hydrological outcomes, there were strong increases in soil moisture ($+36\%$) at large scales, while biocrust suppression of sediment production was clearest at fine (-86%) and medium scales (-67% ; Figure 5). Disturbance advanced the commencement of ponding (-61%) and runoff (-44%), and reduced both infiltration (-37%) and sediment production (-69%). Increasing biocrust cover on intact surfaces was associated with less infiltration (-32%) and sediment production (-76%) but more soil moisture ($+20\%$).

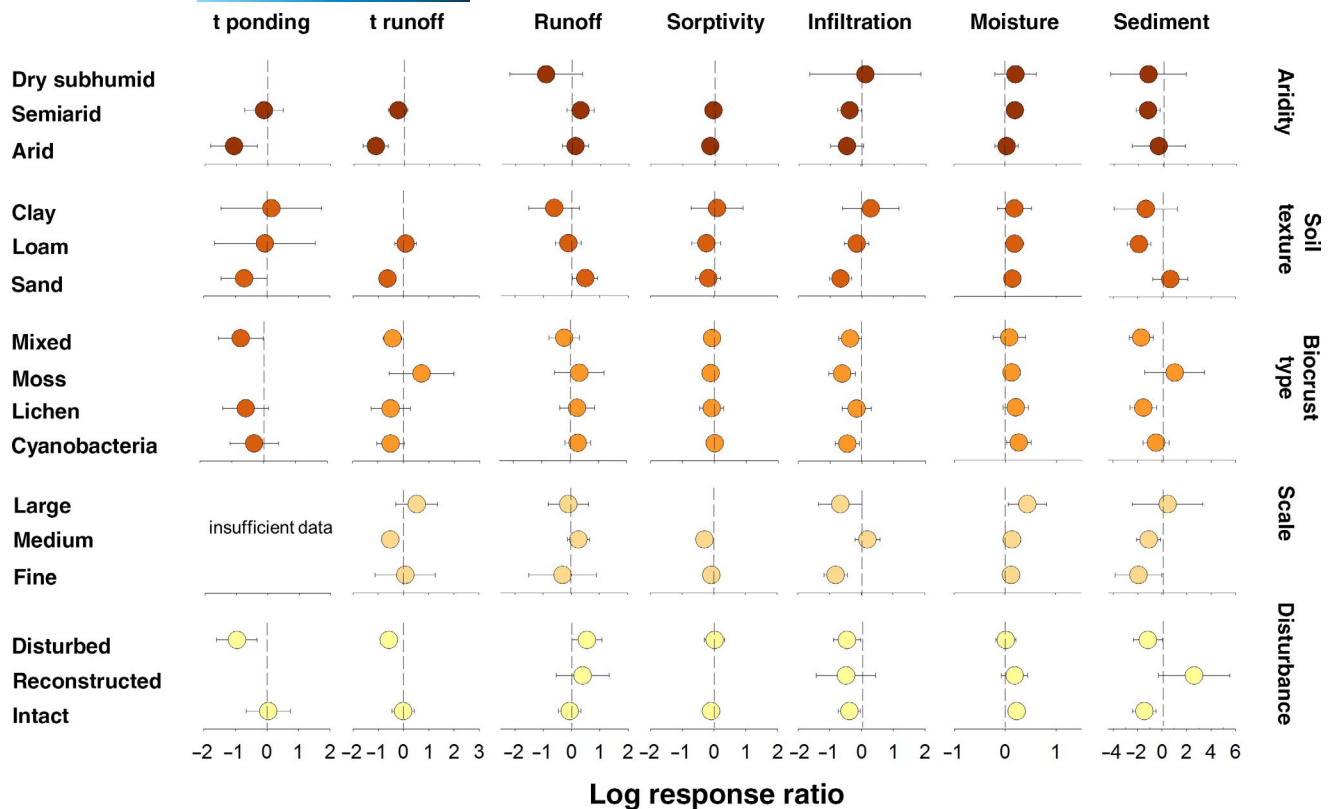


FIGURE 5 Effects of biocrusts, as measured with the log response ratio ($\ln RR \pm 95\% \text{ CI}$), on five hydrological processes: time to ponding (t ponding), time to runoff (t runoff), runoff, sorptivity and infiltration, and two hydrological outcomes: soil moisture (moisture) and sediment production (sediment). Results are separated by different levels of each of the five moderators (1) aridity (arid, semiarid, dry subhumid), (2) soil texture (sand, loam, clay), (3) biocrust type (cyanobacteria, lichen, moss, mixed), (4) measurement scale (fine, medium, large), and (5) disturbance level (intact, reconstructed, disturbed). Significant results are indicated by whether the 95% CI spans the $x = 0$ line. Positive values show that increasing biocrusts cover increased the value of that hydrological process/outcome, while negative values show that increasing biocrust cover reduced it

4 | DISCUSSION

Considered together, the nuances of hydrological processes and outcomes resulting from differences in biocrust type, spatial scale, environmental context, and disturbance levels create a collective picture revealing that runoff and ponding commenced earlier, infiltration and water erosion declined, but soil moisture increased, as biocrust cover increases. We found that soil moisture was greater in the uppermost layers ($<0.5 \text{ mm}$) despite an overall decline in infiltration and no significant difference in runoff. Lower levels of infiltration, yet greater water storage, suggests a false dichotomy of reduced infiltration but greater soil moisture retention, at least in the uppermost layers. The most parsimonious explanation is that biocrusts intercept moisture, restricting deeper penetration of water into the soil, thereby retaining it in the immediate surface layer. This layer aligns with the zone of maximum productivity, nutrient concentrations, and microbial activity, and is a critical zone in dryland soils (Whitford, 2002). Biocrusts may also reduce the diffusion of water vapor by blocking surface pores (George et al., 2003), which we did not measure. This could potentially explain the disconnect between the suppression of infiltration and the enhancement of

soil moisture. Greater surface moisture has important implications for dryland productivity and the provision of essential ecosystem services. Thus, our results provide strong support for the explicit inclusion of biocrusts in global hydrological, Earth systems, and soil loss models.

Consistent with our hypothesis, we found that differences in biocrust type (e.g., moss-, lichen-, or cyanobacteria-dominated) influenced the hydrological response, likely by creating surfaces of differing permeabilities, or gradients in surface friction, and thus a patchwork of microsites that would either shed or retain water (Bowker et al., 2013; Eldridge et al., 2010; Faist et al., 2017). Our data, which evenly spanned these four broad biocrust types (Figure 2), demonstrate several effects of biocrust type on hydrological processes and outcomes. Reductions in sediment production on mixed or lichen biocrusts are likely due to their greater surface rugosity and therefore detention storage (Rodríguez-Caballero et al., 2012). The tendency of cyanobacteria to secrete exopolysaccharides (EPS; Verrecchia, Yair, Kidron, & Verrecchia, 1995), which absorb water (Campbell, 1979) and can block matrix pores (Fischer, Veste, Wiehe, & Lange, 2010), may explain why cyanobacterial biocrusts conducted less water and commenced runoff earlier as their cover

increased (Kidron, Yaalon, & Vonshak, 1999; Mazor, Kidron, Vonshak, & Abeliovich, 1996). Interestingly, we found that the positive effect of biocrusts on soil moisture was most apparent beneath cyanobacterial biocrusts, possibly due in part to their association with physical crusts, which have inherently lower infiltration rates (Issa et al., 2011).

Compared with cyanobacteria, however, lichens tend to retain less water, depending on their morphology and biomass (Blum, 1973), thallus cohesion, and chemical composition (George et al., 2003). Secondary compounds such as acids could also induce hydrophobicity in lichen-dominated biocrusts (Fischer et al., 2010). The lack of a clear hydrological effect of lichens is likely due to trade-offs among factors that either enhance runoff (e.g., hydrophobic lichen chemicals) or ponding (retard runoff) for example, by increasing surface rugosity and detention. For mosses, specialized architecture (e.g., cuculate leaves, leaf hair points) allows many dryland mosses to capture and retain water in leaf-borne structures (lamellae, papillae; Tao & Zhang, 2012). This greater tissue retention (Eldridge & Rosentreter, 2004) may account for lower volumes of water available for infiltration on moss and mixed (moss + cyanobacterial) biocrusts. Thus, biocrust effects on the soil environment can both slow water entry at small scales, but also increase water storage in upper soil layers, and the hydrological consequences are dependent upon the cover and type of biocrusts present. The variability in responses among biocrust types (e.g., moss-dominated vs. lichen-dominated) underscores the need to consider these groups individually, because they are morphologically dissimilar, possess varied internal structures that either suppress or enhance water flow, capture, and retention, and may have strong associations with soils of a certain texture and therefore permeability and erodibility (Bowker, Belnap, Chaudhary, & Johnson, 2008).

We found soil textural effects, as predicted, with a suppression of infiltration on coarser soils. On sandy soils, most hydrological measures of water flow declined with increasing biocrust cover, consistent with our understanding of hydraulic conductivity (Warren, 2001) and field observations of biocrust hydrology (Belnap, Wilcox, Van Scoyoc, & Phillips, 2013; Xiao et al., 2011). Biocrusts form a physical barrier that anchors soil particles and enhance macroaggregation through EPS production. This likely overrides inherent soil erodibility (Bowker et al., 2008) and explains why we found that the effects of increasing biocrust cover most strongly suppressed sediment production on loamy soils (−85%; Figure 5). Other mechanisms include altering inherent soil properties (Gao et al., 2017), increasing detention storage and therefore sediment capture (Chen et al., 2009; Gao et al., 2017; Rodríguez-Caballero et al., 2012), or reducing erodibility by increasing macroaggregate stability (Eldridge, 1998; Eldridge & Kinnell, 1997; Li, Wang, Li, & Zhang, 2002).

Measurement scale might be expected to influence the hydrological outcomes of rainfall because small-scale studies lack features and processes such as patches of vegetation, surface roughness imposed by vascular plants, or channelized flow that influences runoff more at larger spatial scales (Yair et al., 1980). In our meta-analysis, the moderating effects of spatial scale were more difficult to discern because 91% of studies were conducted at the

fine (<0.05 m²) or medium (0.05–10 m²) spatial scales (Figure 2), demonstrating the paucity of global data from large-scale (watershed/catchment) studies. The only clear effect of spatial scale on a hydrological process was a decline (−56%) in infiltration with increasing biocrust cover at fine spatial scales, but no effects at larger scales, thus providing partial support for our hypothesis of a scale effect. Hydrological outcomes were influenced by scale, as increasing biocrust cover was associated with a strong increase in soil moisture (+36%) at large scales, while biocrust suppression of sediment production was clearest at medium scales (−67%; Figure 5). The scale dependency of hydrological responses suggests that future studies should focus on studies at large spatial scales, which are poorly represented in most biocrust hydrological studies, and are needed to adequately represent natural hydrological processes associated with landscape connectivity and redistribution processes (Chamizo et al., 2016; Rodríguez-Caballero, Román, Chamizo, Roncero Ramos, & Cantón, 2019).

Finally, we expected that the extent of surface disturbance would influence the degree to which biocrusts alter hydrological functions, by destroying the biocrusted surface and reducing stability, or by altering the density and size of depressions that capture sediment (Eldridge, 1998). Even though available data were heavily weighted toward intact surfaces (63%; Figure 2), our hypothesis was upheld, and disturbance had context-dependent effects on hydrology, generally reducing the time for water to pond and runoff to commence. Earlier commencement of runoff (−44%) and ponding (−61%), less sediment production (−69%), and reduced infiltration (−37%) on disturbed biocrusted surfaces are likely due to combined effects of surface pore clogging by dispersed material (Faist et al., 2017) and increases in detention storage resulting from surface disruption. Disturbance effects on measures of water flow, however, were mixed, with increasing biocrust cover on intact surfaces associated with less sorptivity and infiltration, more soil moisture, and less sediment production. It is likely that factors unrelated to the soil surface, such as differences in soil texture, measurement scale, or the pretreatment of biocrusts (e.g., scalping, spraying with herbicide; Williams, Dobrowolski, & West, 1995; Zaady, Levacov, & Shachak, 2004), might be influential.

5 | CONCLUDING REMARKS

In summary, our global assessment demonstrates that, despite contextual nuances, biocrusts are essential components of the dryland water puzzle. The results of our study reinforce the view that any potential hydrological effects of biocrusts should consider the linkages among the different hydrological processes and outcomes rather than considering individual responses in isolation. The distribution, movement, and retention of soil water is one of the greatest unknowns in global climate models. Key land use drivers, such as overgrazing and vegetation clearance that cause widespread disturbance and can alter biocrust cover and composition (Ferrenberg, Reed, & Belnap, 2015), are likely to have far-reaching consequences

for hydrological processes and outcomes in drylands. For drylands, which cover nearly half of the world's terrestrial surface and are growing in spatial extent (Huang et al., 2017; Právělie, 2016), it is critical that soil moisture retained by biocrusts is considered in global climate, vegetation and land use models. Accounting for biocrusts and their hydrological impacts can provide us with a more accurate picture of the impacts of climate change on dryland ecosystems and improve our capacity to manage dwindling dryland water supplies in a warmer, drier world.

ACKNOWLEDGEMENTS

This work was conducted as part of the Powell Working Group "Completing the dryland puzzle: creating a predictive framework for biological soil crust function and response to climate change" supported by the John Wesley Powell Center for Analysis and Synthesis, funded by the US Geological Survey. Shinichi Nakagawa and Max Mallen-Cooper guided us through the R code for the meta-analyses. J.B. and S.R. were funded by USGS Ecosystems and Land Use Change Mission Areas, by the US Department of Energy (DESC-0008168), and by the Strategic Environmental Research and Development Program (RC18-1322). J.D. is supported by grants from the Holsworth Wildlife Research Endowment & The Ecological Society of Australia, and a scholarship from China Scholarship Council (No. 201706040073). B.C. is supported by grants from the National Science Foundation (award DEB-1844531) and DePaul University. M.A.B. is supported by a grant from the National Science Foundation (award DEB-1638966). B.W. was supported by the Max Planck Society and a Paul Crutzen Nobel Laureate Fellowship. E.H.-S. was supported by CONACYT grant 251388 B. F.T.M. was supported by the European Research Council (ERC grant agreement 647038 [BIODESERT]) and Generalitat Valenciana (CIDEGENT/2018/041). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTION

D.J.E. wrote the first draft of the manuscript and S.R. wrote a draft of the Introduction. D.J.E., S.K.T., and J.D. compiled and formatted the database, and undertook the data analysis. S.K.T. and C.H. designed the figures and all authors edited and contributed to subsequent drafts. A.A., N.B., J.B., and M.A.B. are co-PIs on the grant that supported this work and also helped with project logistics and organization.

DATA AVAILABILITY STATEMENT

The database compiled and used in this meta-analysis is available from Figshare database <https://doi.org/10.6084/m9.figshare.12478919>.

ORCID

David J. Eldridge  <https://orcid.org/0000-0002-2191-486X>
Matthew A. Bowker  <https://orcid.org/0000-0002-5891-0264>

REFERENCES

- Armas, C., Ordiales, R., & Pugnaire, F. I. (2004). Measuring plant interactions: A new comparative index. *Ecology*, 85, 2682–2686. <https://doi.org/10.1890/03-0650>
- Belnap, J., & Lange, O. L. (2003). Biological soil crusts: Structure, function, and management. In J. Belnap, & O. Lange (Eds.), *Ecological studies* (Vol. 150; pp. 3–30). Berlin, Germany: Springer.
- Belnap, J., Wilcox, B. P., Van Scoyoc, M. W., & Phillips, S. L. (2013). Successional stage of biological soil crusts: An accurate indicator of ecohydrological condition. *Ecohydrology*, 6, 474–482. <https://doi.org/10.1002/eco.1281>
- Blum, O. B. (1973). Water relations. In V. Ahmadjian & M. E. Hale (Eds.), *The lichens* (pp. 381–400). Academic Press. Retrieved from <https://doi.org/10.1016/b978-0-12-044950-7.50016-7>
- Bowker, M. A., Belnap, J., Chaudhary, V. B., & Johnson, N. C. (2008). Revisiting classic water erosion models in drylands: The strong impact of biological soil crusts. *Soil Biology and Biochemistry*, 40, 2309–2316. <https://doi.org/10.1016/j.soilbio.2008.05.008>
- Bowker, M. A., Eldridge, D. J., Val, J., & Soliveres, S. (2013). Hydrology in a patterned landscape is co-engineered by soil-disturbing animals and biological crusts. *Soil Biology and Biochemistry*, 61, 14–22. <https://doi.org/10.1016/j.soilbio.2013.02.002>
- Campbell, S. E. (1979). Soil stabilization by a prokaryotic desert crust: Implications for Precambrian land biota. *Origins of Life*, 9, 335–348. https://doi.org/10.1007/978-94-009-9085-2_8
- Cantón, Y., Solé-Benet, A., De Vente, J., Boix-Fayos, C., Calvo-Cases, A., Asensio, C., & Puigdefábregas, J. (2011). A review of runoff generation and soil erosion across scales in semiarid south-eastern Spain. *Journal of Arid Environments*, 75, 1254–1261. <https://doi.org/10.1016/j.jaridenv.2011.03.004>
- Chamizo, S., Belnap, J., Eldridge, D. J., Cantón, Y., & Issa, O. M. (2016). The role of biocrusts in arid land hydrology. In B. Weber, B. Büdel, & J. Belnap (Eds.), *Biological soil crusts: An organizing principle in drylands. Ecological studies (analysis and synthesis)* (Vol. 226, pp. 321–346). Champ, Switzerland: Springer. Retrieved from https://doi.org/10.1007/978-3-319-30214-0_17
- Chen, N., Liu, X., Zheng, K., Zhang, C., Liu, Y., Lu, K., ... Zhao, C. (2019). Ecohydrological effects of biocrust type on restoration dynamics in drylands. *Science of the Total Environment*, 687, 527–534. <https://doi.org/10.1016/j.scitotenv.2019.06.007>
- Chen, R., Zhang, Y., Li, Y., Wei, W., Zhang, J., & Wu, N. (2009). The variation of morphological features and mineralogical components of biological soil crusts in the Gurbantunggut Desert of Northwestern China. *Environmental Geology*, 57, 1135–1143. <https://doi.org/10.1007/s00254-008-1410-1>
- Cherlet, M., Hutchinson, C., Reynolds, J., Hill, J., Sommer, S., & Von Maltitz, G. (2018). *World atlas of desertification: Rethinking land degradation and sustainable land management*. Luxembourg: Publications Office of the European Union.
- Dunkerley, D. (2010). Ecogeomorphology in the Australian drylands and the role of biota in mediating the effects of climate change on landscape processes and evolution. In P. Bishop & B. Pillans (Eds.), *Australian landscapes* (pp. 87–120). Geological Society Special Publication. London, UK: Geological Society. Retrieved from <https://doi.org/10.1144/sp346.7>
- Eldridge, D. (1998). Trampling of microphytic crusts on calcareous soils, and its impact on erosion under rain-impacted flow. *Catena*, 33, 221–239. [https://doi.org/10.1016/s0341-8162\(98\)00075-7](https://doi.org/10.1016/s0341-8162(98)00075-7)
- Eldridge, D. J., Bowker, M. A., Maestre, F. T., Alonso, P., Mau, R. L., Papadopoulos, J., & Escudero, A. (2010). Interactive effects of three ecosystem engineers on infiltration in a semi-arid Mediterranean grassland. *Ecosystems*, 13, 499–510. <https://doi.org/10.1007/s10021-010-9335-4>
- Eldridge, D., & Kinnell, P. (1997). Assessment of erosion rates from microphyte-dominated calcareous soils under rain-impacted flow. *Soil Research*, 35, 475–490. <https://doi.org/10.1071/s96072>

- Eldridge, D., & Rosentreter, R. (2004). Shrub mounds enhance waterflow in a shrubsteppe community in southwestern Idaho, USA. In A. L. Hild, N. L. Shaw, S. E. Meyer, D. T. Booth, & E. D. McArthur (compilers) (Eds.), *Seed and soil dynamics in shrubland ecosystems proceedings* (pp. 79–83). RMRS-P-31. Ogden, UT: US Department of Agriculture, Forest Service, Rocky Mountains Research Station.
- Eldridge, D., Tozer, M., & Slangen, S. (1997). Soil hydrology is independent of microphytic crust cover: Further evidence from a wooded semiarid Australian rangeland. *Arid Land Research and Management*, 11, 113–126. <https://doi.org/10.1080/15324989709381465>
- Faist, A. M., Herrick, J. E., Belnap, J., Van Zee, J. W., & Barger, N. N. (2017). Biological soil crust and disturbance controls on surface hydrology in a semi-arid ecosystem. *Ecosphere*, 8, e01691. <https://doi.org/10.1002/ecs2.1691>
- Ferrenberg, S., Reed, S. C., & Belnap, J. (2015). Climate change and physical disturbance cause similar community shifts in biological soil crusts. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 12116–12121. <https://doi.org/10.1073/pnas.1509150112>
- Fischer, G., Nachtergaele, F., Prieler, S., Van Velthuisen, H., Verelst, L., & Wiberg, D. (2008). *Global agro-ecological zones assessment for agriculture* (GAEZ 2008). Laxenburg, Austria and Rome, Italy: IIASA and FAO. Retrieved from <http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/>
- Fischer, T., Veste, M., Wiehe, W., & Lange, P. (2010). Water repellency and pore clogging at early successional stages of microbiotic crusts on inland dunes, Brandenburg, NE Germany. *Catena*, 80, 47–52. <https://doi.org/10.1016/j.catena.2009.08.009>
- Gao, L., Bowker, M. A., Xu, M., Sun, H., Tuo, D., & Zhao, Y. (2017). Biological soil crusts decrease erodibility by modifying inherent soil properties on the Loess Plateau, China. *Soil Biology and Biochemistry*, 105, 49–58. <https://doi.org/10.1016/j.soilbio.2016.11.009>
- George, D. B., Roundy, B. A., St. Clair, L. L., Johansen, J. R., Schaalje, G. B., & Webb, B. L. (2003). The effects of microbiotic soil crusts on soil water loss. *Arid Land Research and Management*, 17, 113–125. <https://doi.org/10.1080/15324980301588>
- Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, 80, 1150–1156. [https://doi.org/10.1890/0012-9658\(1999\)080\[1150:tmaorr\]2.0.co;2](https://doi.org/10.1890/0012-9658(1999)080[1150:tmaorr]2.0.co;2)
- HilleRisLambers, R., Rietkerk, M., van den Bosch, F., Prins, H. H., & de Kroon, H. (2001). Vegetation pattern formation in semi-arid grazing systems. *Ecology*, 82, 50–61. [https://doi.org/10.1890/0012-9658\(2001\)082\[0050:vpfisa\]2.0.co;2](https://doi.org/10.1890/0012-9658(2001)082[0050:vpfisa]2.0.co;2)
- Huang, J., Yu, H., Dai, A., Wei, Y., & Kang, L. (2017). Drylands face potential threat under 2°C global warming target. *Nature Climate Change*, 7, 417–422. <https://doi.org/10.1038/nclimate3275>
- IPCC. (2018). Summary for policymakers. In V. Masson-Delmotte, P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P. R. Shukla, ... T. Waterfield (Eds.), *Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty* (pp. 1–32). Geneva, Switzerland: World Meteorological Organization.
- Issa, O. M., Valentin, C., Rajot, J. L., Cerdan, O., Desprats, J. F., & Bouchet, T. (2011). Runoff generation fostered by physical and biological crusts in semi-arid sandy soils. *Geoderma*, 167, 22–29. <https://doi.org/10.1016/j.geoderma.2011.09.013>
- Kidron, G. J., Yaalon, D. H., & Vonshak, A. (1999). Two causes for runoff initiation on microbiotic crusts: Hydrophobicity and pore clogging. *Soil Science*, 164, 18–27. <https://doi.org/10.1097/00010694-199901000-00004>
- Leigh, C., Sheldon, F., Kingsford, R. T., & Arthington, A. H. (2010). Sequential floods drive 'booms' and wetland persistence in dryland rivers: A synthesis. *Marine Environmental Research*, 61, 896–908. <https://doi.org/10.1071/mf10106>
- Li, X., Wang, X., Li, T., & Zhang, J. (2002). Microbiotic soil crust and its effect on vegetation and habitat on artificially stabilized desert dunes in Tengger Desert, North China. *Biology and Fertility of Soils*, 35, 147–154. <https://doi.org/10.1007/s00374-002-0453-9>
- Loik, M. E., Breshears, D. D., Lauenroth, W. K., & Belnap, J. (2004). A multi-scale perspective of water pulses in dryland ecosystems: Climatology and ecohydrology of the western USA. *Oecologia*, 141, 269–281. <https://doi.org/10.1007/s00442-004-1570-y>
- Ludwig, J. A., Wilcox, B. P., Breshears, D. D., Tongway, D. J., & Imeson, A. C. (2005). Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology*, 86, 288–297. <https://doi.org/10.1890/03-0569>
- Mazor, G., Kidron, G. J., Vonshak, A., & Abeliovich, A. (1996). The role of cyanobacterial exopolysaccharides in structuring desert microbial crusts. *FEMS Microbiology Ecology*, 21, 121–130. <https://doi.org/10.1111/j.1574-6941.1996.tb00339.x>
- Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being: General synthesis*. Washington DC: Island Press.
- Muggeo, V. M., & Muggeo, M. V. M. (2017). Package 'segmented'. *Biometrika*, 58, 516. <https://cran.r-project.org/doc/Rnews/>
- Nakagawa, S. (2015). Missing data: Mechanisms, methods and messages. In G. A. Fox, S. Negrete-Yankelevich, & V. J. Sosa (Eds.), *Ecological statistics: Contemporary theory and application* (pp. 81–105). Oxford, UK: Oxford Scholarship Online.
- Nakagawa, S., Noble, D. W., Senior, A. M., & Lagisz, M. (2017). Meta-evaluation of meta-analysis: Ten appraisal questions for biologists. *BMC Biology*, 15, 1–14. <https://doi.org/10.1186/s12915-017-0357-7>
- Nakagawa, S., & Santos, E. S. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, 26, 1253–1274. <https://doi.org/10.1007/s10682-012-9555-5>
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Neumann, K., Sietz, D., Hilderink, H., Janssen, P., Kok, M., & van Dijk, H. (2015). Environmental drivers of human migration in drylands – A spatial picture. *Applied Geography*, 56, 116–126. <https://doi.org/10.1016/j.apgeog.2014.11.021>
- Prävalle, R. (2016). Drylands extent and environmental issues. A global approach. *Earth-Science Reviews*, 161, 259–278. <https://doi.org/10.1016/j.earscirev.2016.08.003>
- Rodríguez-Caballero, E., Cantón, Y., Chamizo, S., Afana, A., & Solé-Benet, A. (2012). Effects of biological soil crusts on surface roughness and implications for runoff and erosion. *Geomorphology*, 145, 81–89. <https://doi.org/10.1016/j.geomorph.2011.12.042>
- Rodríguez-Caballero, E., Román, J. R., Chamizo, S., Roncero Ramos, B., & Cantón, Y. (2019). Biocrust landscape-scale spatial distribution is strongly controlled by terrain attributes: Topographic thresholds for colonization in a semiarid badland system. *Earth Surface Processes and Landforms*, 44, 2771–2779. <https://doi.org/10.1002/esp.4706>
- Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9, 671–675. <https://doi.org/10.1038/nmeth.2089>
- Shachak, M., Pickett, S. T., Boeken, B., & Zaady, E. (1999). Managing patchiness, ecological flows, productivity, and diversity in drylands: Concepts and applications in the Negev Desert. In M. Shachak & T. Hoekstra (Eds.), *Arid lands management – Toward ecological sustainability* (pp. 254–263). Urbana and Chicago, IL: University of Illinois Press.
- Sloat, L. L., Gerber, J. S., Samberg, L. H., Smith, W. K., Herrero, M., Ferreira, L. G., ... West, P. C. (2018). Increasing importance of precipitation variability on global livestock grazing lands. *Nature Climate Change*, 8, 214–218. <https://doi.org/10.1038/s41558-018-0081-5>

- Tao, Y., & Zhang, Y. M. (2012). Effects of leaf hair points of a desert moss on water retention and dew formation: Implications for desiccation tolerance. *Journal of Plant Research*, 125, 351–360. <https://doi.org/10.1007/s10265-011-0449-3>
- Verrecchia, E., Yair, A., Kidron, G. J., & Verrecchia, K. (1995). Physical properties of the psammophile cryptogamic crust and their consequences to the water regime of sandy soils, north-western Negev Desert, Israel. *Journal of Arid Environments*, 29, 427–437. [https://doi.org/10.1016/s0140-1963\(95\)80015-8](https://doi.org/10.1016/s0140-1963(95)80015-8)
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48. <https://doi.org/10.18637/jss.v036.i03>
- Wang, L., Manzoni, S., Ravi, S., Riveros-Iregui, D., & Caylor, K. (2015). Dynamic interactions of ecohydrological and biogeochemical processes in water-limited systems. *Ecosphere*, 6, 1–27. <https://doi.org/10.1890/es15-00122.1>
- Warren, S. D. (2001). Synopsis: Influence of biological soil crusts on arid land hydrology and soil stability. In J. Belnap & O. L. Lange (Eds.), *Biological soil crusts: Structure, function, and management*. Springer. https://doi.org/10.1007/978-3-642-56475-8_26
- Weber, B., Büdel, B., & Belnap, J. (2016). *Biological soil crusts: An organizing principle in drylands. Ecological studies (analysis and synthesis)* (Vol. 226). Cham, Switzerland: Springer. Retrieved from <https://doi.org/10.1007/978-3-319-30214-0>
- Whitford, W. G. (2002). *Ecology of desert systems*. San Diego, CA: Academic Press. Retrieved from [https://doi.org/10.1644/1545-1542\(2003\)084<1122:EODS>2.0.CO;2](https://doi.org/10.1644/1545-1542(2003)084<1122:EODS>2.0.CO;2)
- Williams, J. D., Dobrowolski, J. P., & West, N. (1995). Microphytic crust influence on interrill erosion and infiltration capacity. *Transactions - American Society of Agricultural Engineers*, 38, 139–146. <https://doi.org/10.13031/2013.27822>
- Xiao, B., Wang, Q., Zhao, Y., & Shao, M. (2011). Artificial culture of biological soil crusts and its effects on overland flow and infiltration under simulated rainfall. *Applied Soil Ecology*, 48, 11–17. <https://doi.org/10.1016/j.apsoil.2011.02.006>
- Yair, A., Lavee, H., Bryan, R., & Adar, E. (1980). Runoff and erosion processes and rates in the Zin valley badlands, Northern Negev, Israel. *Earth Surface Processes and Landforms*, 5, 205–225. <https://doi.org/10.1002/esp.3760050301>
- Zaady, E., Levacov, R., & Shachak, M. (2004). Application of the herbicide, Simazine, and its effect on soil surface parameters and vegetation in a patchy desert landscape. *Arid Land Research and Management*, 18, 397–410. <https://doi.org/10.1080/15324980490497483>
- Zomer, R. J., Trabucco, A., Bossio, D. A., & Verchot, L. V. (2008). Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems & Environment*, 126, 67–80. <https://doi.org/10.1016/j.agee.2008.01.014>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Eldridge DJ, Reed S, Travers SK, et al.

The pervasive and multifaceted influence of biocrusts on water in the world's drylands. *Glob Change Biol*. 2020;00: 1–12. <https://doi.org/10.1111/gcb.15232>