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

Running title: Biocrusts and hydrological function

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DJE wrote the first draft of the manuscript and SR wrote a draft of the Introduction. DJE, SKT and JD compiled and formatted the database, and undertook the data analysis. SKT and CAH designed the figures and all authors edited and contributed to subsequent drafts. AJA, NNB, JB, and MAB are co-PIs on the grant that supported this work and also helped with project logistics and organization.

Data accessibility statement:

Supporting information is included in this manuscript. The data have been lodged with Figshare https://10.6084/m9.figshare.10247012

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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 2997 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 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 (hyper-arid, 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; Prăvălie, 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 to 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 mineralisation 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 emphasise 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, 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 prior 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 'runoff'], sorptivity, infiltration) and two hydrological outcomes (sediment production, soil water storage; Table 1 and Appendix S1). The biocrust literature suggests that hydrological effects *sensu lato* are 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 biocrusts 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 to 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.

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

Processes and outcomes	**Description**	***n***
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 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

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 (Fig. 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 to which our keywords captured critical biocrust hydrology literature. Suitable records needed to meet the following requirements for inclusion in our study: 1) restricted to terrestrial systems in drylands, in other words, where the aridity index (precipitation/potential evapotranspiration [P/PET]) was < 0.65, 2) contain quantitative data on at least one of the seven hydrological measures, and 3) include 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: 1) time taken for water to pond on the surface (time to ponding) or 2) to commence runoff (time to runoff), 3) sorptivity (the early stage of infiltration; rate or volume), 4) steady-state infiltration (the latter stage of infiltration; hereafter ‘infiltration’; rate or volume), 5) runoff (rate or volume), and two hydrological outcomes: 6) soil moisture, and 7) 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 stabilised and is regulated largely by hydraulic conductivity. Data presented in figures from published articles were extracted with ImageJ (Schneider et al., 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.

Calculating effect size

To determine the effects of biocrusts on hydrological processes and outcomes, we used the log response ratio $\ln RR = \ln(X_{Lower}/X_{Higher})$ 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 lnRR represent situations where hydrological processes and outcomes declined with an 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: bare (≤ 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 lnRR 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 lnRR for 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 (≤ 10% biocrusts cover; n = 382).

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 = 0.79; 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: 1) a unique ID for each reference, 2) the order of the data within the data file, and 3) a measure of the difference in biocrust cover between any two contrasts. To calculate this measure of differences, we used the RII (Relative Interaction Intensity, Armas, Ordiales, & Pugnaire, 2004) of biocrust cover (i.e., higher cover – lower cover)/(higher cover + lower cover), which relativises the effect of absolute values of changes in cover on our hydrological components, allowing, for example, a 10% change in cover from 0-10% 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 & Santos, 2012; Nakagawa et al., 2017), 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: 1) 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 1- (P/PET) so that higher values of aridity corresponded to greater dryness. 2) Soil texture data (sand, loam, clay) were obtained from each paper; when data were missing, we contacted individual authors or used the HWSD database (6% of cases; Fischer et al., 2008) to derive a value. 3) Biocrust type was classified as cyanobacteria-, lichen-, moss-dominated, or mixed. This characterisation 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. 4) 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 m^2, generally petri dish or small rainfall simulator, medium (0.05 – 10 m^2; large rainfall simulators) and large (> 10 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. 5) 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. Study identity and the order that the data were incorporated as random effects. 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 $P < 0.05$. 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 cm, 2-5 cm and >5 cm.

Publication bias was assessed using 1) funnel plots, 2) Egger regression and 3) 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, Fig. S4.2 in Appendix S4).

3. RESULTS

Our literature search yielded 183 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 2997 contrasts of an effect of biocrusts on the seven hydrological variables from five continents (Asia, Europe, Australia, North America, Africa; Fig. 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 (Fig. 2a) or from sandy or loamy soils (85%; Fig. 2b). Studies were relatively evenly distributed among the four biocrust types (Fig. 2c). Ninety-one percent of studies were conducted at the fine (< 0.05 m^2) or medium (0.05 – 10 m^2) spatial scales (Fig. 2d) and 63% were conducted on intact surfaces (Fig. 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 (Fig. 3; Table S4.1). 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 ± 95% CI; Fig. S6.3 in Appendix S6). Further, despite lower infiltration, the uppermost (< 0.5 cm) soil surface stored 60% more water than depths of 2-50 cm (Fig. 4).

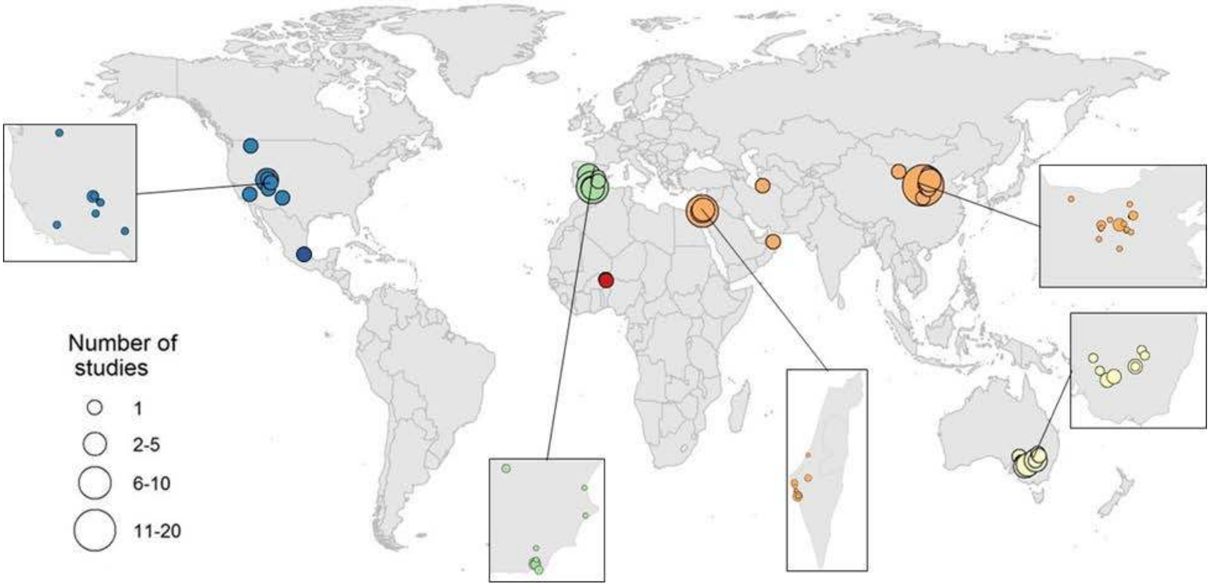

Figure 1. Map of the global distribution of sites used in the meta-analysis. Circle size represents the number of studies from each region. Inset maps show more site details for the main hotspots of biocrusts hydrological research.

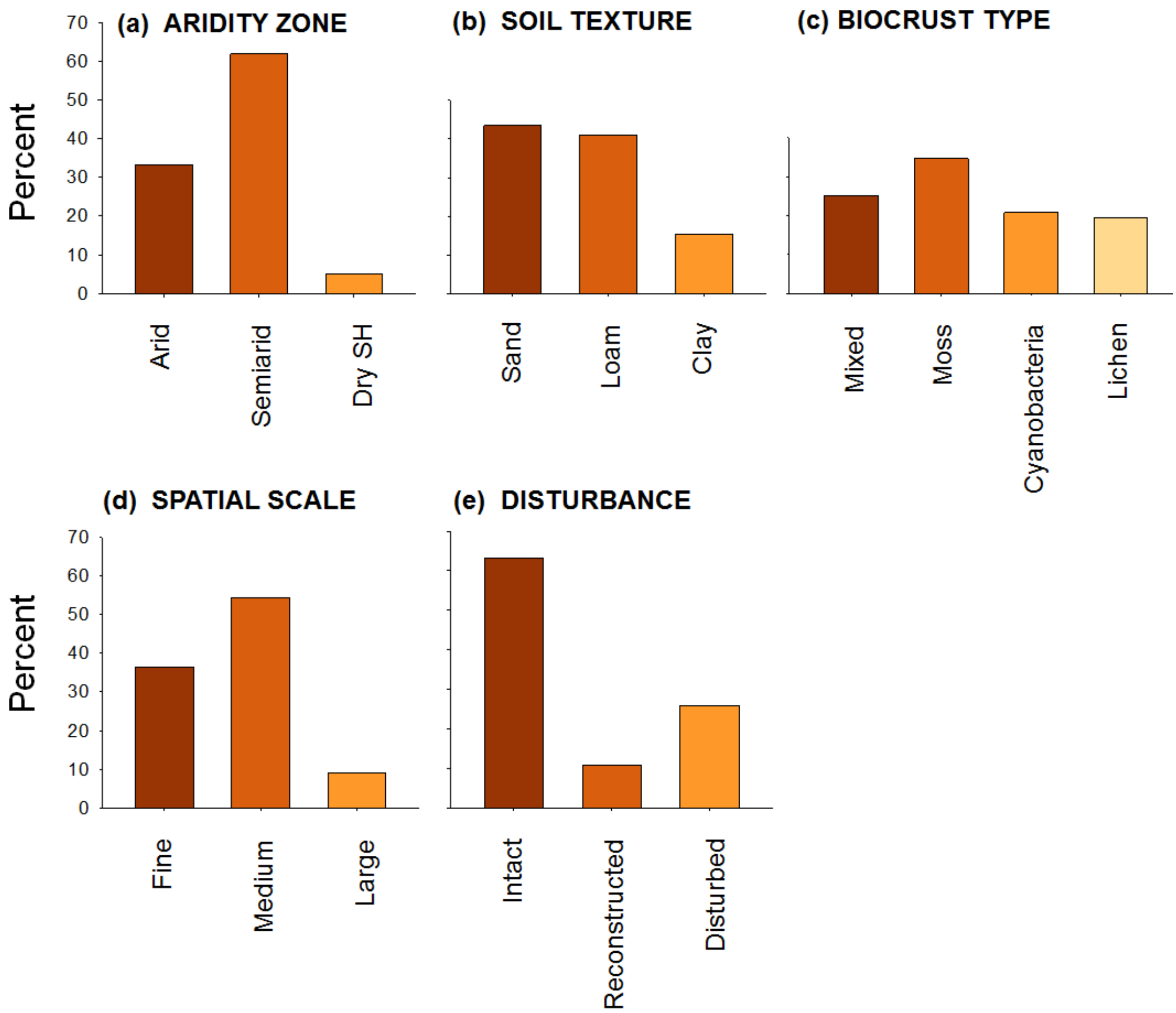

Figure 2. Percentage of records by (a) Aridity zone, (b) Soil texture, (c) Biocrust type, (d) Spatial scale and (e) Disturbance. SH = subhumid.

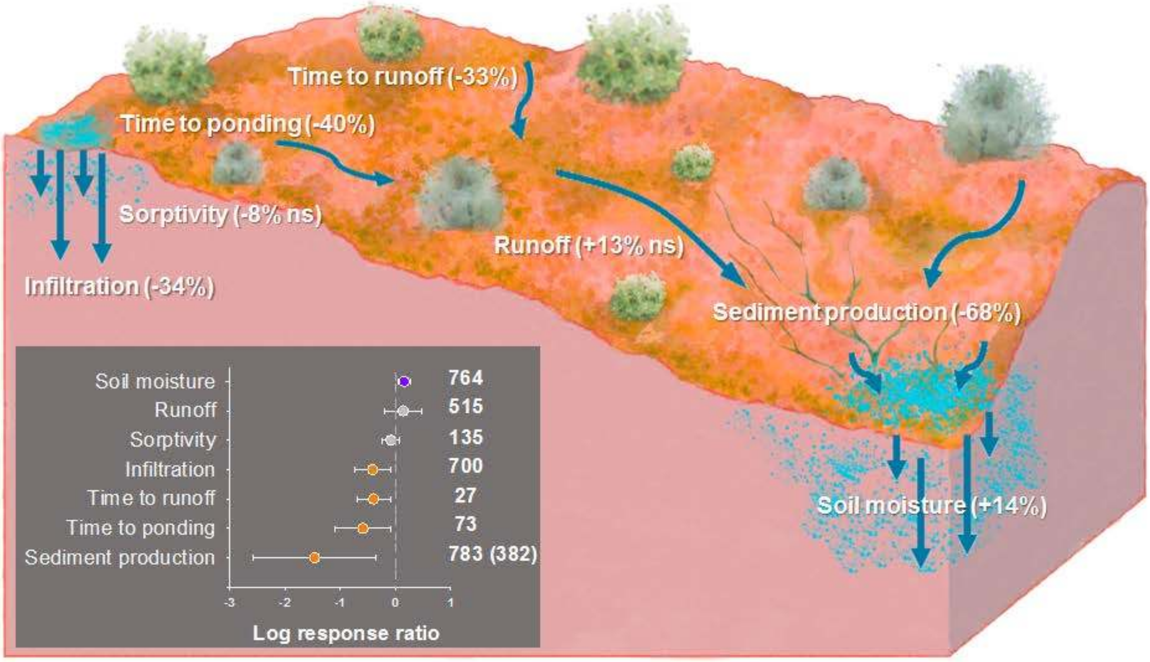

Figure 3. Schematic diagram of a dryland landscape showing the main processes and outcomes of water movement, soil moisture and sediment production and the overall percentage change resulting from greater biocrust cover. Asterisks indicate a significant (*P* < 0.05) effect increasing biocrust cover. Insert diagram shows the mean value of the log response ratio (± 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).

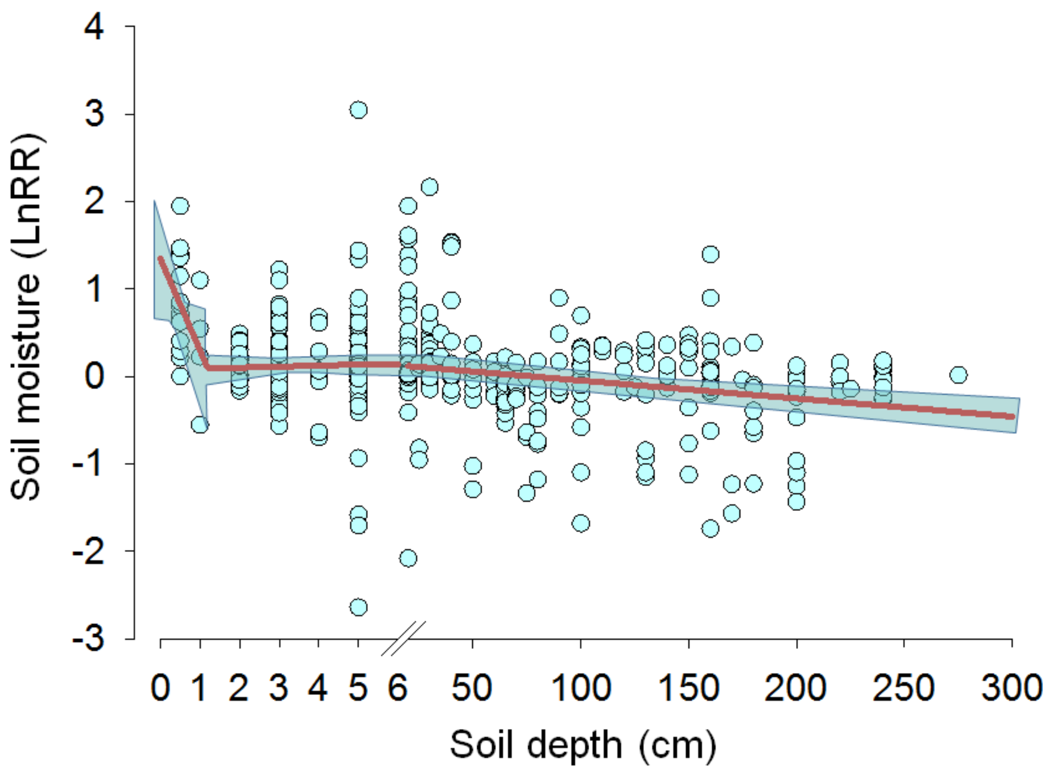

Figure 4. Changes in the log response ratio (lnRR) of soil moisture in relation to changing soil depth. The segmented regression analysis indicated three models, with a significant decline in soil moisture from 0.5-1 cm (*P* = 0.045), but no differences from 1 to 5 cm and 5 to 300 cm depths.

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 lower in semiarid (-33%) and arid (-39%) areas (Fig. 5). The suppressive effect of increasing biocrust cover on sediment production 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 (Fig. 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 (Fig. 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 (Fig. 5), and the effects of increasing biocrust cover most strongly suppressed sediment production on loamy soils (-85%; Fig. 5).

We detected several effects of biocrust type on hydrological processes and outcomes. For example, sediment production was reduced most on mixed (-82%) or lichen (-78%) biocrusts (Fig. 5), and the time to runoff commenced later 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 (Fig. 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%; Fig. 5). Disturbance delayed the commencement of ponding (-61%) and runoff (-44%), and reduced both infiltration (-37%) and runoff (-42%). Increasing biocrust cover on intact surfaces was associated with less infiltration (-32%) and sediment production (-76%) but more soil moisture (+20%).

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 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 vapour 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.

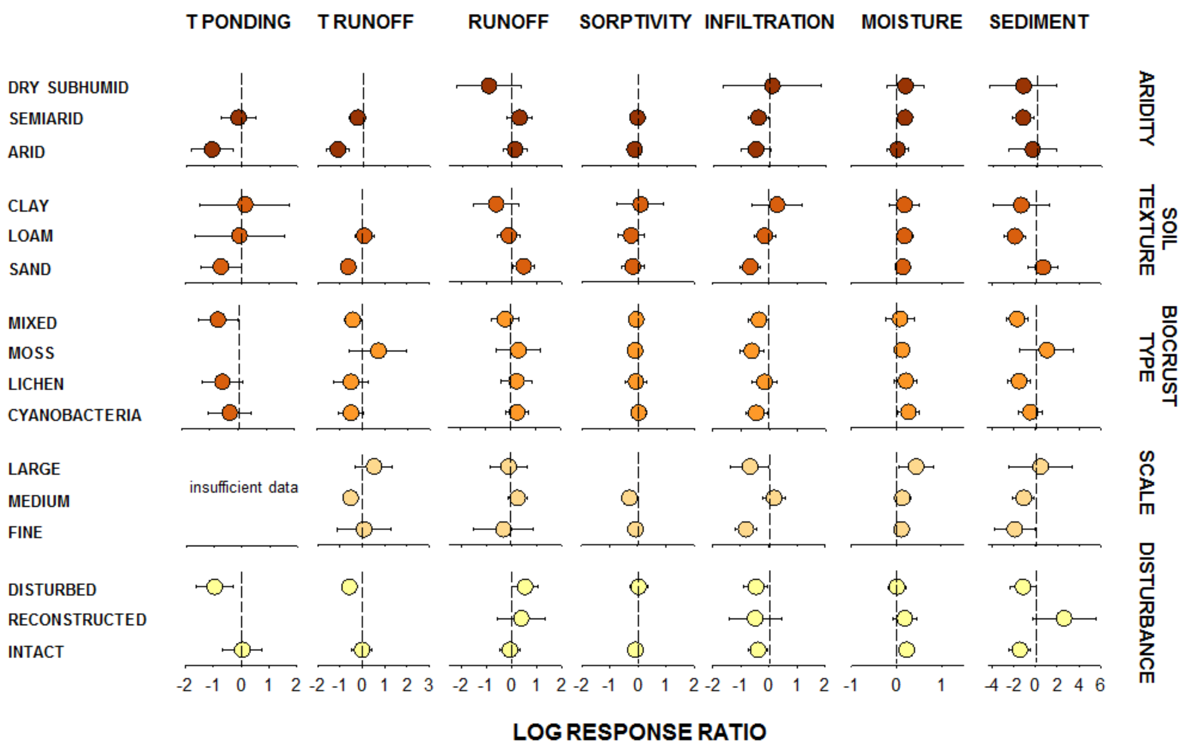

Figure 5. Effects of biocrusts, as measured with the log response ratio (lnRR ± 95% CI), on five hydrological processes: time to ponding (t ponding), time to runoff (t runoff), runoff, sorptivity and infiltration, and two hydrological outcomes: soil moisture (moisture) and sediment production (sediment). 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.

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 (Fig. 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 EPS (Verrecchia, Yair, Kidron, & Verrecchia, 1995), which absorbs 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 between factors that either enhance runoff (e.g. hydrophobic lichen chemicals) or ponding (retard runoff) for example, by increasing surface rugosity and detention. For mosses, specialised 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 finer soils, likely due to silt and clay dispersion beneath biocrusts (Cantón et al., 2011), which leads to the formation of physical crust (Chamizo, Cantón, Lázaro, & Domingo, 2013), mimicking the effects of cyanobacterial exopolysaccharides (EPS; Campbell, 1979). 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%; Fig. 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 macro-aggregate stability (Eldridge & Kinnell, 1997; Eldridge, 1998; Li et al., 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 m^2) or medium (0.05 – 10 m^2) spatial scales (Fig. 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%; Fig. 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 towards intact surfaces (63%; Fig. 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 runoff (-42%), 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 pre-treatment 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; Prăvălie, 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.

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Biocrusts are widely distributed globally, and have marked effects on ecosystem properties and processes.

A global assessment of biocrusts on hydrology revealed that they reduced the time for water to pond, on the surface, commence runoff, infiltrate and produce sediment, but increased soil moisture storage in the topsoil.

Biocrust effects on hydrology varied markedly with soil texture, aridity, biocrust type, spatial scale and level of disturbance.

Our synthesis provides novel insights into the magnitude, processes, and contexts of biocrust effects in drylands; information that is critical for sustainable management of Earth's dwindling dryland water supplies.

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