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COMMENT

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Comment on 'Kidron, G. J. (2018). Biocrust research: A critical view on eight common hydrological-related paradigms and dubious theses. *Ecohydrology*, e2061'

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1 | INTRODUCTION

Kidron (2018) uses a straw man argument in an attempt to debunk eight putative hydrological-related paradigms he believes to be "common among hydrologists, ecologists, or microbiologists that investigate biocrusts." These paradigms relate to the roles of physical crusts and vascular plants in biocrust development, the major drivers (climate, porosity, hydrophobicity, and exopolysaccharides) of hydrology (infiltration and runoff), and the effect of mosses on hydrology and therefore vascular plants. We see two major problems with his arguments. First, they assume that the paradigms in question are generally accepted by biocrust researchers. Second, they are based on Kidron's (2018) world view of biocrusts, which has largely been informed by his own studies from a single, distinctly unique area of sand dunes at the Nizzana Research Site in the Negev Desert, Israel. This narrow focus and the selective use of published material disqualify his arguments. Our collective experience, based on more than 250 person years of biocrust research, and more than 700 scientific publications on biocrusts from all continents including Antarctica, indicates that, far from the straw man arguments proposed by Kidron (2018), there is no evidence to support the existence of a unifying theory that captures the global effects of biocrusts on hydrology. Our collective works demonstrate that, contrary to claims by Kidron (2018), the hydrological effects of biocrusts are strongly nuanced, varying with, but not limited to, differences in ecological context, landscape position, site condition, crust type and composition, climatic zone, soil texture and porosity, surface morphology, and spatial scale (reviewed in Weber, Büdel, & Belnap, 2016). Below, we critically analyse each of Kidron's (2018) paradigms, providing rigorous empirical evidence to show that none represent commonly held views among the biocrust research community.

2 | PARADIGM 1: BIOCRUSTS REQUIRE PHYSICAL CRUSTS AND OR A LAYER OF DUST FOR ESTABLISHMENT

Biocrusts often colonize physical crusts, which are commonly interspersed with biocrusts (Chamizo, Belnap, Eldridge, Cantón, & Malam

Issa, 2016; Chamizo, Cantón, Lázaro, Solé-Benet, & Domingo, 2012; Malam Issa et al., 2011). Biocrusts require a degree of physical stability, which can arise from an association with not only physical soil crusts but also soil fines, organic matter or aggregates, vascular plant stems, or, as Kidron (2018) suggests, exopolysaccharides (EPS) secreted by the biocrust organisms themselves (Hu, Liu, Smestad Paulsen, Petersen, & Klaveness, 2003; Mugnai et al., 2018). The stabilizing effects of EPS have been known for decades (Chesters, Attoe, & Allen, 1957; Mazor, Kidron, Vonshak, & Abeliovich, 1996; Underwood, Paterson, & Parkes, 1995; Van Ancker, Jungerius, & Mur, 1985). Similarly, many studies, often cited by Kidron, attest to dust capture by biocrusts (Danin & Ganor, 1991; Felde, Chamizo, Felix-Henningsen, & Drahorad, 2018; Felde, Peth, Uteau-Puschmann, Drahorad, & Felix-Henningsen, 2014; McTainsh & Strong, 2007; Reynolds, Belnap, Reheis, Lamothe, & Luiszer, 2001; Williams, Buck, & Beyene, 2012), a mechanism that is important for biocrust stability and nutrient cycling. Kidron (2018) asserts that soil fines can hasten biocrust colonization and growth (Mugnai, Rossi, Chamizo, Adessi, & De Philippis, 2020; Rozenstein et al., 2014; Zaady, Katra, Barkai, Knoll, & Sarig, 2017) but is citing the absence of biocrusts from playas at the Nizzana site as proof that fines do not facilitate biocrust formation. Playa surfaces, however, are biologically hostile, subject to periods of extreme sedimentation or inundation, and often highly saline (Blume, Beyer, Pfisterer, & Felix-Henningsen, 2008), a point overlooked in this paradigm. In summary, a critical review of the literature reveals that biocrusts are often interwoven with physical crusts and dust, but physical crusts are not necessarily precursors to biocrust establishment.

3 | PARADIGM 2: PLANT ESTABLISHMENT IS NECESSARY FOR BIOCRUST ESTABLISHMENT ON DUNES

We know from recent extensive meta-analyses that the effects of biocrusts on plants are complex, strongly nuanced, and driven by crust type and biocrust traits (Havrilla et al., 2019). An overwhelming body of evidence points to the opposite view to that advanced in Paradigm 2 by Kidron (2018). Best available evidence indicates that biocrusts prime surface soils with water and nutrients and facilitate the establishment of vascular plants (Lan et al., 2014; Langhans, Storm, & Schwabe, 2009; X. J. Li et al., 2008; Rodríguez-Caballero, Chamizo, Roncero-Ramos, Román, & Cantón, 2018). We also know that some moss and lichen species benefit from their association with moisture-rich habitats, which could be provided by nurse plants (Jiang et al., 2018), but could equally result from shading by rocks, or their location at lower landscape positions that receive additional run-on water (Lan et al., 2014; Williams, Buck, Soukup, & Merkler, 2013; Yair, 1990). Thus, it is clear that plant establishment per se is not a precursor for biocrust establishment on dunes.

4 | PARADIGM 3: DEVELOPMENTAL STAGES OF BIOCRUSTS ARE OFTEN REGARDED AS SUCCESSIONAL STAGES

Paradigm 3 is based on the observation that filamentous cyanobacteria are the first pioneering photosynthetic organisms to colonize disturbed soils, hence, the putative link to biocrust successional stage, irrespective of desert type. As biocrusts develop, the trajectory of change and the resulting species composition will depend on abiotic factors such as climate, soils, and specific microclimatic conditions. In more mesic environments, high biomass and developmental stage are likely synonymous. In more arid environments, however, later stages of development are likely to be limited by the lack of moisture, so that biocrusts will remain dominated by cyanobacteria or cyanolichens. In many environments, a mixture of different patch types and resource levels will result in a mixture of successional stages within the same site, a phenomenon acknowledged by Kidron (2018). Thus, Paradigm 3 applies to some environments (Belnap & Eldridge, 2003) but is not globally consistent (e.g., Chilton, Neilan, & Eldridge, 2018). Successional theory advances that earlier successional species condition a site to favour late-successional species (Bowker, 2007). However, we are unaware of any empirical evidence to show that succession occurs in biocrusts past the cyanobacterial stage. Potential mechanisms by which biocrust species might affect different species directly by facilitation or competition (Li et al., 2013; Maestre, Callaway, Valladares, & Lortie, 2009; Soliveres & Eldridge, 2020) or indirectly by altering site conditions or facilitating different species are poorly understood (Soliveres & Eldridge, 2020). Nonetheless, if, as stated by Kidron (2018), "the role of cyanobacteria as precursor of lichen-dominated crusts is undermined," one cannot help but wonder where the photobionts in lichens originate from. In summary, the literature indicates that developmental and successional stages are synonymous in some contexts, but not in others, a view widely held within the biocrust research community.

5 | PARADIGMS 4–8: CLIMATE-DRIVEN CRUST MORPHOLOGY DETERMINES CRUST HYDROLOGY (PARADIGM 4); SOIL PORES AND EXOPOLYSACCHARIDES DETERMINE INFILTRATION (PARADIGMS 5 & 7); SOIL PORES AND HYDROPHOBICITY DETERMINE RUNOFF (PARADIGMS 5 & 6), AND MOSSES IMPEDE INFILTRATION AND PERENNIAL PLANT GROWTH (PARADIGM 8)

Paradigms 4–8 deal with what Kidron (2018) sees as the major drivers of hydrology (*sens. lat.*) or specific hydrological processes (infiltration and runoff). Given that the mechanisms behind these moderators exhibit several commonalities, we deal with these paradigms together.

That climate drives hydrology via crust morphology (Paradigm 4) is only partially correct and certainly not a universal paradigm. Climate can affect freeze–thaw relationships, alter porosity and sorptivity, and sometimes influence runoff indirectly through controls on vascular plant–biocrust composition (Belnap, 2006). Climate (aridity) can also influence moss cover (Ferrenberg, Reed, & Belnap, 2015), which may alter retention time (Eldridge & Rosentreter, 2004). Rainfall intensity can also affect hydrology, by influencing the runoff coefficient (the proportion of rainfall that does not infiltrate) and therefore the partitioning of rainfall between runoff and infiltration.

However, a critical examination of the literature reveals that climate is but one of many factors affecting hydrology (Belnap, 2006). Other equally important moderators of hydrology, include, but are not limited to, crust composition (Chamizo, Cantón, Lázaro, et al., 2012), which can influence surface roughness (Rodríguez-Caballero, Cantón, Chamizo, Afana, & Solé-Benet, 2012), hydrophobicity (Lichner et al., 2018), soil texture (Chamizo, Cantón, Miralles-Mellado, & Domingo, 2012), spatial scale (Cantón et al., 2011; Chamizo, Cantón, Rodríguez-Caballero, Domingo, & Escudero, 2012), and level of disturbance (Eldridge, 1998; Faist, Herrick, Belnap, Van Zee, & Barger, 2017). Thus, it is inconceivable that climate-driven morphology alone can be invoked as the major driver of hydrology. The assertion that "macro pores determine infiltration on biocrusted surfaces is however highly questionable" (Kidron, 2018) is inconsistent with the large body of evidence that these subsurface vesicular pores have a major impact on water infiltration by drastically reducing soil hydraulic conductivity (Dietze, Bartel, Lindner, & Kleber, 2012; Turk & Graham, 2011; Young, McDonald, Caldwell, Benner, & Meadows, 2004). But even if no vesicular pores exist within (or underneath) biocrusts, they still affect the properties of the pore network of their host soil (Coppola et al., 2011; Felde et al., 2014; Malam Issa, Défarge, Trichet, Valentin, & Rajot, 2009; Miralles-Mellado, Cantón, & Solé-Benet, 2011), which clearly has a strong impact on matter fluxes, including water movement. We acknowledge, however, that many other factors such as climate, topography, surface roughness, spatial scale, and soil texture drive infiltration and therefore runoff. Since porosity is only one of many factors affecting hydrological function, reductions in total pore volume might be compensated for by changes in other hydrological drivers such as surface roughness or water repellency or pore shape and connectivity (a statement that we already made in Felde et al., 2014). Overall, therefore, there is strong evidence to suggest that soil pores determine runoff (Paradigm 5).

Paradigm 6 contends that runoff is a result of hydrophobicity (Kidron, 2018; Section 2.6). Biocrust hydrophobicity is highly temporally and spatially variable (Tighe, Haling, Flavel, Young, & Moya-Larano, 2012) and, contrary to claims by Kidron (2018), has been shown to depend on soil moisture content (Rodríguez-Caballero, Cantón, Chamizo, Lázaro, & Escudero, 2013; Yang et al., 2014) and to occur at sub-critical levels (low levels of hydrophobicity; Tillman, Scotter, Wallis, & Clothier, 1989) at the Nizzana Research Site (Keck, Felde, Drahorad, & Felix-Henningsen, 2016). This response of hydrophobicity (e.g., de Jonge, Jacobsen, & Moldrup, 1999; King, 1981) is thought to be related to the reorientation of amphiphilic molecules (Hallett, 2008). Like porosity and climate, hydrophobicity is but one of many factors influencing biocrust hydrology.

The effects of EPS on soil hydrology (Paradigm 7) are complex and not completely understood. EPS in biocrusts are complex macromolecules comprising different monosaccharide fractions with different molecular weight distributions and consequently different capability to interact with soil particles and with water molecules (Rossi, Mugnai, & De Philippis, 2018). It is not unreasonable, therefore, that any effects of EPS on hydrology should vary across different studies (e.g., Rossi, Potrafka, Garcia-Pichel, & De Philippis, 2012; cf. Colica et al., 2014), particularly where those studies are from different soil types, with diverse crust types of varying morphologies, and markedly different EPS chemical and macromolecular characteristics. Any claim that EPS determine infiltration (Kidron, 2018) is only part of the truth, which is that the hydrological effects of biocrusts are strongly nuanced and vary widely with abiotic and biotic factors.

Finally, Paradigm 8 contends that mosses impede infiltration and therefore perennial plant growth. There is almost no empirical evidence to support or invalidate this paradigm, so claims that this view is "common among hydrologists, ecologists, or microbiologists" are at best spurious. It is generally acknowledged, however, that mosses have variable effects on infiltration, either enhancing (Wu, Hasi, & Wugetemole,, & Wu, X., 2012) or suppressing (Xiao, Zhao, Wang, & Li, 2015) infiltration depending on ecological context and the nature of the moderators (soil texture, climate, level of disturbance, spatial scale, etc.) described above. Mosses can retain water due to the presence of specialized leaf architecture (leaf hair points, lamellae, and papillae) (Pan et al., 2016), which could reduce infiltration to deeper layers (Eldridge & Rosentreter, 2004), but this likely varies with moss species, seasonality, and soil type (Wu et al., 2012). Moss effects on the survival and growth of vascular plants are also variable and will depend on the balance of these contrasting effects. However, a global meta-analysis indicates that their overall effect on vascular plant performance is positive, but effects on germination are negative (Havrilla et al., 2019). There is little support for the contention therefore that mosses impede perennial plant growth.

6 | CONCLUDING REMARKS

It is clear from the preceding discussion that the eight putative paradigms advanced by Kidron (2018) cannot be upheld nor are they commonly held among hydrologists, ecologists, or microbiologists that investigate biocrusts. However, we are thankful that Kidron (2018) has formally published his viewpoint because it gives us the opportunity to critically examine the veracity of such arguments, an important stage in the scientific process. Any proposal for paradigms that report global phenomena for such idiosyncratic communities of organisms as biocrusts would require an examination of the literature across the whole spectrum of biocrust distribution and environmental settings. Unfortunately, Kidron's (2018) "critique" is unashamedly heavily reliant on his own knowledge of desert systems, largely from one dune field in southern Israel. In attempting to globalize the effects of biocrusts on hydrology, Kidron (2018) risks simplifying nuanced and complex conditions providing junior researchers a narrow view of biocrust effects on hydrology, while ignoring the full spectrum of effects in different environmental and experimental contexts and scenarios. This generalization risks trivializing the science of biocrust hydrology and ignores decades of established research undertaken globally on biocrusts.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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