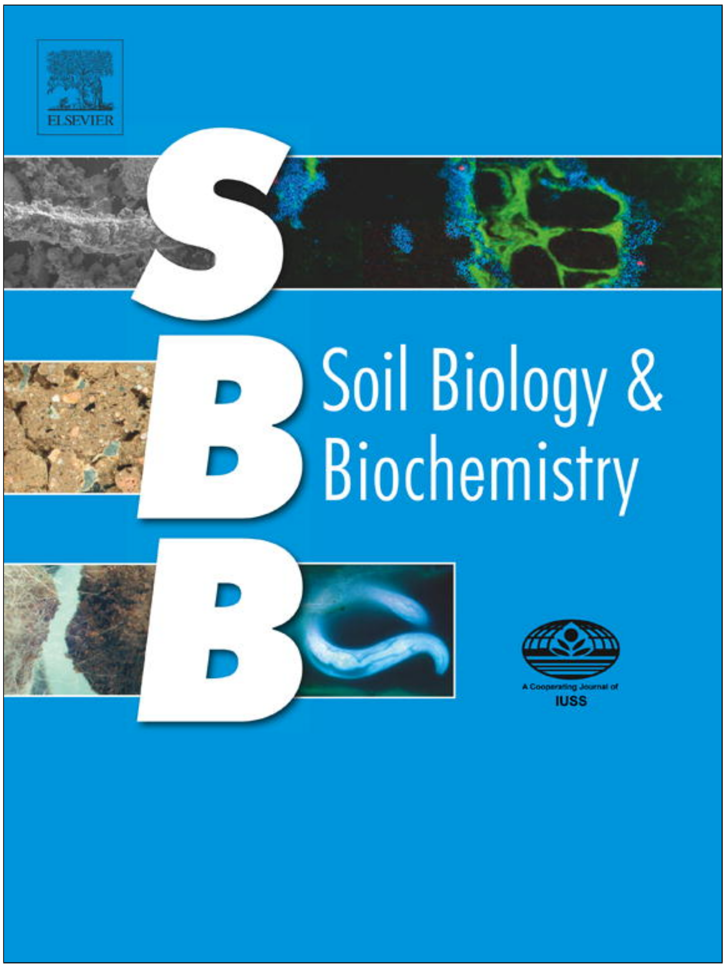

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Hydrology in a patterned landscape is co-engineered by soil-disturbing animals and biological crusts

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A B S T R A C T

Water redistribution has a profound influence on dryland ecosystem function. This hydrological function is largely regulated by ecosystem engineers including biological soil crusts (biocrusts) which produce run-off, and burrowing animals, such as the greater bilby, whose pits capture water. We estimated the relative importance of these two ecosystem engineers in determining infiltration rates in a system where dune slopes shed water to adjacent interdune swales to maximize overall productivity. Also, we determined which biocrust property was most hydrologically important: total cover, composition, patch aggregation or spatial heterogeneity. While both biocrusts and burrowing animals equally affected the overall infiltration through macro- and micropores (under ponding), only biocrusts were important for the infiltration specifically *via* micropores (under tension). Of the studied biocrust properties, community composition was the strongest influence such that the greater the prevalence of early successional biocrust patches, the greater the infiltration rate. Greater total cover of biocrusts reduced infiltration, and the spatial properties were relatively unimportant. Although bilbies and biocrusts comparably influenced infiltration under ponding at the microscale, realistic cover of bilby pits at the landscape scale is unlikely to strongly impair the hydrological function of dunes. Reintroduction of the endangered bilby may enhance nutrient cycling and plant recruitment *via* its seed and resource capturing pits, without a concomitant disruption of hydrological function. In contrast, removal of biocrusts caused by, e.g., livestock trampling, is expected to strongly enhance infiltration in the run-off areas, strongly reducing ecosystem productivity at the landscape scale.

1. Introduction

In drylands, primary producers convert soil moisture stocks into energy inputs, driving many subsequent ecosystem processes (Noy-Meir, 1973). Soil moisture stocks are much more variable than would be expected if precipitation infiltrated soil evenly due to water redistribution across the soil surface (Noy-Meir, 1973). The spatial arrangement of landscape patches determines movement of water among and within patches (Bastian, 2001; Wu and Hobbs, 2002). In dryland ecosystems on multiple continents, banded spatial patterning is common (Tongway et al., 2001). In banded systems, upslope areas with relatively low vegetation cover are aligned parallel to lower bands of denser vegetation (Eldridge, 1999; Malam Issa et al., 1999). The upslope areas generate run-off, which is then intercepted and sequestered as it passes though the downslope run-on areas. The amount of water that is redistributed to run-on areas is of utmost importance in promoting overall productivity of the ecosystem, and likely depends on characteristics of the upslope run-off zones such as water repellency, and prevalence of soil disturbance. The soil disturbance activity of livestock is a widespread and well-studied factor which can retard infiltration by destroying soil surface structure, or promote it by destroying water repellent surfaces (Graetz and Tongway, 1986; Yates et al., 2000). In contrast, the soil disturbances of burrowing animals, and their landscape-level importance, are less well understood. In the ungrazed run-off areas of our system, the water repellency of biological soil crusts (biocrusts, hereafter), and the soil disturbance activity of the greater bilby (*Macrotis lagotis*), an endangered ground-foraging mammal,

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potentially co-regulate water redistribution but it is unknown which is the stronger influence or whether bilby reintroduction efforts could disrupt hydrological function.

Biological soil crusts are a common soil surface community of bryophytes, lichens, cyanobacteria and other organisms prevalent in drylands (*reviewed in* Belnap, 2006). These biocrusts act as ecosystem engineers (*sensu* Jones et al., 1994) because they modulate the availability of resources, such as water to other species by altering the physical state of the environment (Jones et al., 1994). The tendency for biocrusts to retard or enhance water infiltration is known to depend on the total amount of biocrust and the specific mix of organisms comprising the crust (Malam-Issa et al., 1999; Belnap, 2006; Eldridge et al., 2010). The spatial aggregation of biocrusts has been shown to be modestly related to soil properties such as bulk density and therefore porosity, which are relevant to the hydrological properties of soils (Maestre et al., 2005). In addition, spatial heterogeneity of biocrusts could influence infiltration by shuttling water to preferred pathways, or by influencing burrowing microfauna. The important role of biocrusts on ecosystem hydrology, however, may be compromised by their sensitivity to disturbances, such as hoof action associated with livestock grazing (Eldridge, 1998; Read et al., 2008; Jimenez Aguilar et al., 2009), or burrowing activity (Eldridge et al., 2010).

Burrowing animals, therefore, may act as additional ecosystem engineers, affecting both biocrusts and ecosystem hydrology (Eldridge et al., 2010). Burrowing animals would be expected to indirectly alter run-off generation by altering biocrusts, as was shown in the interaction between rabbits and biocrusts in a semi-arid steppe in Spain (Eldridge et al., 2010). Because foraging pits also provide an entry point for water to infiltrate into soil, they would also be expected to have a direct effect, even in the absence of biocrusts (James et al., 2009). One such prolific soil-disturbing animal that was once common over large areas of continental Australia is the greater bilby. Since European settlement, they have been nearly extirpated due predation by feral predators (fox, cat) and habitat destruction. Local reintroduction efforts are now being made (Moseby and O'Donnell, 2003). The reintroduction of bilbies into large, fenced, predator-proof conservation reserves is an example of the application of large-scale, experimental ecosystem engineering. Ecosystem engineering has been employed for the purposes of restoring ecological function (Byers et al., 2006), but it is unknown whether bilby-focused conservation will reinforce or retard ecosystem functioning.

We exploit a hydrological system of roughly linear run-off generating dunes and the intervening, run-on intercepting swales. We investigated the roles of two ecosystem engineers, bilbies and biocrusts, on run-off generating dune slopes where greater ecosystem function is linked to the export of water, and adjacent interdune swales where greater ecosystem function is linked to the capture of water. We posed the following questions: 1. What is the relative importance of these two ecosystem engineers in two contrasting hydrological environments? 2. Can the biocrust effects on infiltration processes be partitioned into effects of four different biocrust properties: total cover, community structure, spatial aggregation, and spatial heterogeneity? 3. Can the effects of bilby activity on infiltration rates be partitioned among their direct effects, and their indirect effects *via* destruction of biocrusts? 4. At the landscape scale, is the reintroduction of bilbies likely to impair the run-off transport system from dunes to more productive swales? Further, how might the run-off disruption capacity of bilby burrows compare to the more widespread impacts associated with livestock grazing? An understanding of the relative importance of likely regulators of this water redistribution system will enhance our ability to balance extractive land uses, overall productivity, and the management of endangered species for conservation.

2. Materials and methods

2.1. Study area

We conducted all sampling within the Australian Wildlife Conservancy's Scotia Sanctuary in western New South Wales, Australia (33°08′13″S, 141°11′33″E). The sanctuary is notable in that, historically, it was only grazed by domestic livestock as late as the mid-1900s, and then only lightly, as many areas are remote from water sources. Consequently, the area represents an environment that is very close to pre-European conditions (Westbrooke, 2012). The landscape is typical of calcareous sand plains and is characterized by linear dunes, and interdune swales composed of red earths of older alluvial origin (Walker, 1991; Eldridge and Tozer, 1996). This land system comprises dune crests, dune slopes, and swales. Dune slopes typically function as run-off zones, shedding water to the lower swales which are zones of accumulation of resources. Both dune slopes and swales support biocrusts (Downing and Selkirk, 1993), although their composition differs, depending on position: dune slopes tend to support morphologically simpler cyanobacterial crusts, and swales are occupied by a richer community of lichens, mosses and liverworts. Properties of dune and swale soils are tabulated in Appendix 1 of the Supplementary material.

The Australian Wildlife Conservancy has reintroduced multiple endangered mammals, including the bilby. The bilby is a nocturnal native marsupial of similar size to the European rabbit. Like the rabbit, it acts as an allogenic ecosystem engineer due to its prolific digging of foraging pits and burrows (Moseby and O'Donnell, 2003). Its omnivorous diet leads it to dig conical to cylindrical pits for various invertebrates, plant materials and sometimes vertebrates, that are distinguishable by shape from other types of pits (Gibson, 2001). Exotic competitors and predators of the bilby, such as the red fox and the European rabbit have been removed from large parts of the sanctuary, including the area we studied. Bilbies were released into these large landscape-level exclosures in 2008, and since then, their numbers have increased dramatically (AWC unpublished data), resulting in an increasing number of their distinctive pits in both dune slopes and swales.

2.2. Sampling design

We sampled 72 microsites distributed across three dune slope-swale systems in an effort to disperse our sampling. Within each dune slope or swale we intentionally sampled the maximal variation present in a regression-type design based upon a randomization of all possible combinations of: presence and prevalence of forage pits, total biocrust cover, patchy and homogenous spatial patterning of biocrusts, and dominance of biological crusts by different functional groups (Fig. 1). For example, one random combination might be a microsite lacking forage pits, with high, homogenous biocrust cover, dominated by mosses. Surveyors searched the site for a sampling location that best matched these selection criteria, then selected others based on other random permutations of these criteria. All criteria were judged relative to the site; for example, if a site tended toward low cover, then a "high cover" microsite might have less cover than at another site. All of these microsite properties were later quantified. The strength of this sampling strategy is that it diminishes correlation among variables in a dataset, so that their influences on a variable of interest, e.g. infiltration, are independent. Using appropriate multivariate modeling techniques, we can then partition effects of, for example, biocrust patchiness and biocrust cover.

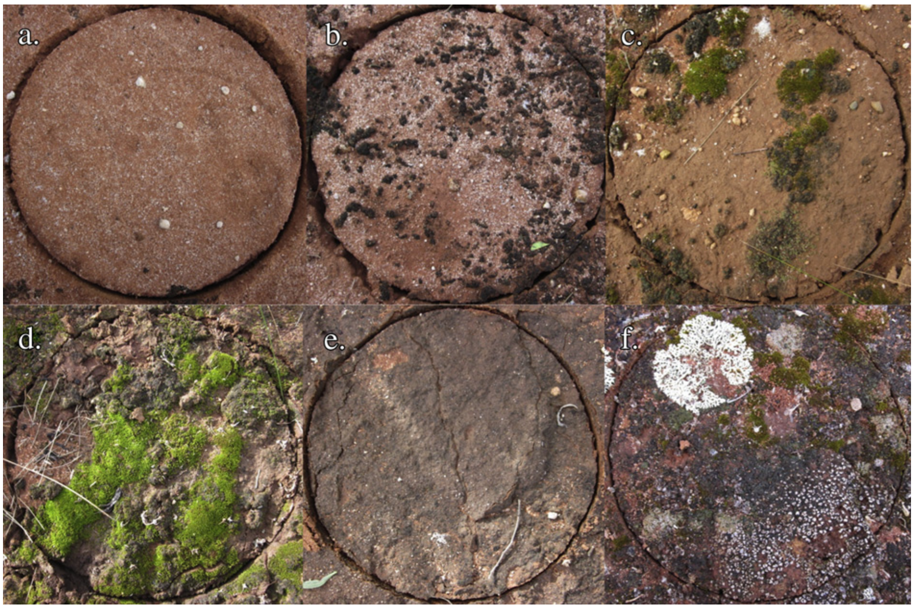

Fig. 1. Illustration of the wide variety of total cover, spatial patterning, and functional group composition observed in biocrusts: a. no biocrust cover, b. low cover of "black crusts", low aggregation, fine-scale heterogeneity, c. low cover of moss crusts, highly aggregated coarse-scale heterogeneity, d. high cover of moss crusts, highly aggregated coarse-scale heterogeneity, e. near-total cover of homogeneous cyanobacterial crust, f. very high homogenous cover of a variety of functional groups including mosses and various lichens. Soil properties are tabulated in Appendix 1 in the Supplemental material.

2.3. Characterization of micro-landscape properties

In each microsite we estimated total biocrust cover by six functional groups: 1. Cyanobacterial crusts: soils exhibit grayish pigmentation consistent with cyanobacteria, 2. Black crusts: A black pigmented conglomeration of difficult to separate dense cyanobacteria, gelatinous lichens, and scattered squamulose lichens e.g. *Collema coccophorum*, *Peltula australiensis*, *Heppia despreauxii*, 3. Crustose lichens: lichens of crustose genera such as *Diploschistes*, *Aspicilia*, and *Caloplaca*, 4. Squamulose lichens: lichens of squamulose genera such as *Psora*, *Endocarpon* and *Placydium*, 5. Foliose lichens: represented by a single species, *Xanthoparmelia reptans*, 6. Liverworts: liverworts primarily of the genus *Riccia*, 7. Mosses: various short-statured mosses of the genera *Barbula*, *Didymodon*, and *Gigaspermum*, among others. Cover ranged from nearly 0 to nearly 100%. We also visually estimated the cover of bilby-disturbed soil, which ranged from 0 to 60%.

We estimated two elements of the spatial patterning of biocrusts, heterogeneity and spatial aggregation. We accomplished this by using high resolution photographs of each microsite with a grid of 100–1.5 cm^2 cells overlaid. In each grid cell, we estimated the total biocrust cover, regardless of functional group. As a measure of the among-cell variability of a microsite (heterogeneity), we calculated the standard deviation of the cover estimates of all 100 grid cells. Spatial aggregation was measured using the spatial analysis by distance indices (SADIE) method (Perry et al., 1999). SADIE calculates an index of aggregation (I_a) based on the total distance in the space that each grid cell would have to be moved to achieve an arrangement where all like values were contiguous. The I_a is obtained by dividing the distance values by the average distance value in permutations. Thus, a value of 1 indicates a random distribution of cover values in space. An aggregated sample has an $I_a > 1$, and a regularly distributed sample (exhibiting spatial disaggregation of repellency) has an $I_a < 1$. The higher the I_a the more spatially aggregated the sample. SADIE analyses were performed for each sample using 5000 permutations with the freeware described by Perry et al. (1999; www.iacr.bbsrc.ac.uk/pie/sadie).

2.4. Infiltration measurements

We measured two primary components of infiltration, sorptivity and steady-state infiltration. Sorptivity is the product of the depth of water absorption and the square root of time, and is dependent on soil water content and diffusivity. Steady-state infiltration, also known as infiltration capacity, is the rate of infiltration per unit cross-sectional area and unit hydraulic gradient. In an operational sense, steady-state infiltration is the rate at which water flow through the soil becomes constant.

Sorptivity and steady-state infiltration are, respectively, the early and late stages of infiltration, and are measured with paired disk permeameters (Perroux and White, 1988). Both components of infiltration were measured at two supply potentials; −40 mm (tension) and +10 mm (ponded; Perroux and White, 1988). Thus, our four primary response variables were sorptivity under ponding ($Sorptivity_{ponding}$), sorptivity under tension ($Sorptivity_{tension}$), steady-state infiltration under ponding ($SSI_{ponding}$), and steady-state infiltration under tension ($SSI_{tension}$). Interpretation of the difference between measurements under ponding and tension rely upon the distinction between matrix pores and macropores. Matrix pores occur between individual mineral grains and between soil particles, and are generally not biogenic. Macropores are larger pores, generally 0.7 mm or more in diameter, and are formed by plant roots and soil fauna. Macropores are extremely important for transferring water, oxygen, and nutrients through the soil (Bouma, 1992). When measurements are conducted under tension, a negative pressure is applied, and flow is restricted to the matrix pores only and water is prevented from entering macropores. Specifically, at a tension of −40 mm, flow is restricted to pores less than 1 mm in diameter (Wilson and Luxmore, 1988). Under ponding, a positive pressure is created (for example, +10 mm), and water flows through both macropores and matrix pores. Therefore, by using both permeameters at both supply potentials (+10 mm and −40 mm), we can partition the amount of water flow through micropores and macropores. A fourth response variable was calculated from these data. Infiltration theory indicates that the ratio of sorptivity under ponded conditions to sorptivity under tension is a useful index of the relative contribution of macropores to total water flow (White, 1988). This ratio, hereafter referred to as macroporosity, therefore indicates the extent to which water flow through the soil is driven by macropores, and is very ecologically informative, as macropores are indicative of soils with a high biological activity or large macroarthropod populations (White, 1988).

2.5. Statistical analyses and modeling

2.5.1. Data reduction

To create a summary variable representing community composition, we ordinated our data of proportional cover of different biocrust functional groups by using non-metric multidimensional scaling based upon Bray–Curtis distance in PC-ORD 4.0 (MJM Software Design, Gleneden Beach, Oregon). Because the biocrust composition was different in dune slopes and swales, we analyzed both matrices separately. Prior to ordination we applied a type of double relativization (McCune and Grace, 2002): 1. We purged the data of the influence of total cover by expressing the cover of each functional group proportionally, 2. We equalized the influence of each functional group on the analysis by rescaling the abundance of each functional group from 0 to 1. In both dunes and swales, we obtained a 3-dimensional ordination and overlaid a second matrix of the various infiltration variables we had measured. One by one we rotated the ordination to maximize its correlation with one of the infiltration measures, then saved the axis scores for the samples for use in later analyses.

2.5.2. Structural equation modeling

We used structural equation modeling to test and parameterize an *a priori* conceptual model. This method is particularly useful for partitioning direct and indirect effects that variables have on others in a systems context (Grace, 2006). The process begins with the formulation of an *a priori* conceptual model of the causal interrelationships among variables (Shipley, 2000). The proposed model structure is fit to a dataset and parameterized. A key parameter is the path coefficient, mathematically related to a regression weight or partial correlation coefficient, which estimates the influence that one variable has on another. Probability tests are employed to determine to what degree these coefficients differ from zero. Our conceptual model stated that various aspects of infiltration ($SSI_{ponding}$, $SSI_{tension}$, $Sorptivity_{ponding}$, $Sorptivity_{tension}$, macroporosity) are directly negatively influenced by biocrusts, and positively influenced by bilby foraging activity. Although our sampling design intentionally decreases the correlation between bilby activity and biocrusts, we also hypothesized that bilby forage activity may influence crust properties. We hypothesized that the biocrust effect could be decomposed and partitioned into effects due to total cover, community structure, and patchiness.

To emphasize differences between the hydrologically-distinct water shedding dune slopes and water accumulating swales, we employed a multigroup modeling approach (Grace, 2006). This approach starts with the assumption that all parameters are equal among the two groups. A goodness of fit test is employed to test this assumption. By viewing residuals of individual parameters, the modeler begins relaxing constraints (allowing a parameter to differ among groups) one by one until a reasonable goodness of fit is obtained. We relaxed parameters until improvements in fit were no longer observed (corresponding to a P value of 0.05–0.10).

2.5.3. Modeling infiltration at the macroscale

To determine the likely effects of bilbies on hydrological function at the macroscale, we re-ran our structural equation models and estimated the means and intercepts. This gave us a complete set of regression slopes and intercepts with which to make model projections. Because the slope terms for biocrust spatial properties were trivial, these terms were left out. To generate a predicted infiltration rate, we required values of biocrust cover, proportional abundance of biocrust functional groups, and cover of foraging pits at landscape scales. We obtained these values of the predictors from two additional datasets documenting: 1) the macroscale percent cover of bilby and other animal burrows both before and after bilby reintroduction, on several swales and dunes (Eldridge et al., 2012), 2) the macroscale percent cover and functional group composition of biocrusts on multiple dunes and swales (Eldridge unpublished data). We used these values to solve the regression models, and estimate $SSI_{ponding}$ and $Sorptivity_{ponding}$, while varying bilby burrow cover according to four scenarios: 1) no burrows, 2) mean burrow abundance prior to bilby reintroduction, 3) mean burrow abundance after bilby reintroduction, and 4) burrow abundance equal to the most extreme observation. The interpretation of these simulations is enhanced when the magnitude of burrow effects is compared relative to other forces; most notably, livestock grazing, which is a key degrading process in drylands globally. To make this comparison, we also developed the four scenarios above in combination with a 50% reduction of the total biocrust, and a doubling of the preponderance of earlier successional functional groups at the expense of later successional groups. Because grazing impacts often reduce biocrust cover by much more than 50%, this is a conservative simulation of what is commonly seen under typical grazing regimes (Eldridge et al., 2006). We focus on the measurements under ponding because they account for infiltration through both macro- and micropores, which is what determines run-off rates in the field. In these simulations we assumed simplistically that all animal diggings (inclusive of goannas and echidnas) function hydrologically similarly to those of bilbies.

Whenever infiltration rates are lower than the rate of rainfall delivery, run-off should occur. The very high values of $Sorptivity_{ponding}$ would suggest that run-off is not occurring when rain falls on dry soils as rainfall intensity would need to be unrealistically high. Thus we made the assumption that virtually all run-off events occur when rain falls on previously hydrated soils, such as in a scenario of successive storms, or long duration storms, thus the key parameter from our models relevant to run-off is $SSI_{ponding}$. In order to estimate the likelihood of different durations of run-off events for each of the eight scenarios, we input the $SSI_{ponding}$ estimates obtained from the different models above into the rainfall-frequency-intensity calculator provided by the Australian Government Bureau of Meteorology (http://www.bom.gov.au/hydro/has/cdirswebx/cdirswebx.shtml), using a range of different event durations from 5 to 410 min. The calculator outputs the average frequency of such an event, which can be converted into annual probability.

3. Results

3.1. Effects of biocrusts and bilbies on microscale infiltration

In the case of infiltration measurements under ponding (though both macro- and micropores), parameter estimates for dunes and swales did not differ (Table 1, Fig. 2). Models of sorptivity and SSI were also very similar to each other, and both explained a considerable proportion of the variance in infiltration ($R^2 = 0.38$ and 0.44, respectively). Under ponding, infiltration was promoted in both habitats, by bilby pits ($r = 0.47$ in all cases) meaning that water export from runoff zones would be diminished. The total biocrust effect was slightly lower ($r = 0.34$–0.40; Table 1), but it is reasonable to state that the two engineers codetermine infiltration properties under ponding.

Table 1
Standardized effects of bilbies and biocrust attributes on six aspects of infiltration on swales and dunes, and variation explained (R^2). |Biocrust| = the composite biocrust effect on a given infiltration variable, in this case the sign in uninterpretable and the absolute value of this effect is given. Bilby direct effects on infiltration are those independent of any alterations of biocrusts. Bilby indirect effects are those expressed *via* the alteration of biocrust properties. All other effects are signed. Probabilities that an effect differs from zero are given in bold superscript when <0.05, alongside the corresponding path coefficients in bold.

		Bilby total	Bilby direct	Bilby indirect	|Biocrust|	Biocrust composition	Biocrust cover	Biocrust aggregation	Biocrust heterogenity	R^2
$Sorptivity_{ponding}$	Swale	0.51	**$0.47^{<0.001}$**	0.04	**$0.34^{<0.001}$**	**$0.36^{<0.001}$**	0.07	−0.02	0.04	0.38
	Dune	0.51	**$0.47^{<0.001}$**	0.04	**$0.34^{<0.001}$**	**$0.36^{<0.001}$**	0.07	−0.02	0.04	0.38
$Sorptivity_{tension}$	Swale	0.12	0.09	0.03	0.33	0.16	**$-0.27^{0.02}$**	−0.21	0.13	0.12
	Dune	0.04	0.08	−0.04	0.48	0.15	**$-0.26^{0.02}$**	−0.19	−0.21	0.33
$SSI_{ponding}$	Swale	0.53	**$0.47^{<0.001}$**	0.06	0.40	**$0.41^{<0.001}$**	0.16	0.11	0.06	0.44
	Dune	0.53	**$0.47^{<0.001}$**	0.06	0.40	**$0.41^{<0.001}$**	0.16	0.11	0.06	0.44
$SSI_{tension}$	Swale	0.15	0.05	0.1	**$0.55^{0.02}$**	**$0.35^{0.002}$**	**$-0.28^{0.03}$**	−0.14	0.20	0.31
	Dune	0.01	0.03	−0.02	**$0.48^{0.03}$**	**$0.25^{0.002}$**	**$-0.18^{0.03}$**	−0.10	−0.24	0.23
Macroporosity	Swale	0.31	**$0.27^{0.02}$**	0.03	**$0.43^{<0.001}$**	**$0.38^{<0.001}$**	**$0.33^{0.003}$**	0.15	0.09	0.28
	Dune	0.31	**$0.27^{0.02}$**	0.03	**$0.43^{<0.001}$**	**$0.38^{<0.001}$**	**$0.33^{0.003}$**	0.15	0.09	0.28

For infiltration under tension (matrix pores only), overall variance explained was lower than that for measurements under ponding, and also differed among dunes and swales (Table 1). Infiltration under tension was clearly most strongly influenced by biocrusts ($r = 0.33–0.55$; Table 1, Fig. 2).

Biocrusts also exerted a strong influence on macroporosity (Table 1), while bilby pits exerted a lesser effect promoting macroporosity ($r = 0.27$). Our model explained about 28% of the variation in macroporosity in both dune and swale.

3.2. *Direct and indirect effects of bilbies on microscale infiltration*

Almost the entire total effect of bilbies on infiltration was due to direct effects, rather than effects due to alteration of biocrust properties (Fig. 2, Table 1). Bilby burrows primarily reduced cover and increased heterogeneity and spatial aggregation, but did not strongly influence composition, the most important biocrust determinant of infiltration.

3.3. *Partitioning individual effects of biocrust properties on microscale infiltration*

In the case of Sorptivity and SSI under ponding, the role of biocrusts was almost totally determined by composition. The particular compositions which favored or retarded infiltration were different in dune and swale habitats (Figs. 3 and 4). On dunes, cyanobacterial crusts were associated with faster infiltration, and black crusts with slower infiltration and thus greater water export capability. On swales, cyanobacteria were again associated with faster infiltration, but it was squamulose lichens which were most strongly associated with slower infiltration.

Infiltration under tension was clearly most strongly influenced by biocrusts, with biocrust cover promoting potential water export in dunes, (Table 1), and a combination of biocrust cover and composition influencing infiltration on swales (Fig. 2). On swales, crustose lichens retarded infiltration but “black” crusts promoted it (Fig. 4). Also in the models of infiltration under tension, the effect of biocrust heterogeneity on infiltration was positive in the swales but negative in the dunes. These effects were not clearly distinct from zero, but they were different from each other.

The biocrust effect on macroporosity was attributable to strong effects of both composition and cover. The compositional effects were very similar to those for infiltration under ponding.

3.4. *Modeled effects of bilbies and biocrusts on macroscale hydrological function*

We estimated baseline $Sorptivity_{ponding}$ and $SSI_{ponding}$ with no animal burrows at 65.5/12.2 mm h^{-1} on dunes and 44.8/7.8 mm h^{-1} on swales. Although cover of foraging pits was only about 1% prior to the reintroduction of bilbies (dune = 0.80%; swale = 1.15%), these burrows have a detectable effect on infiltration, increasing

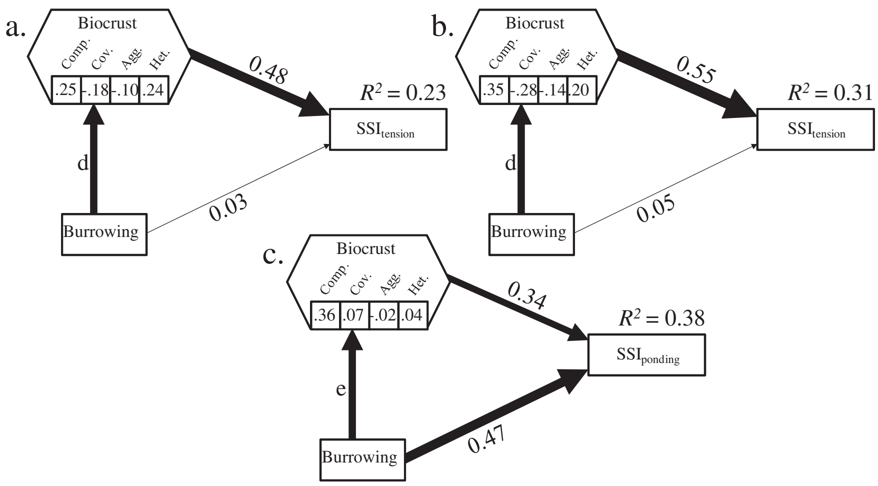

Fig. 2. Selected structural equation models for $SSI_{tension}$ on dunes (a) and swales (b), and $SSI_{ponding}$ on both dunes and swales (c). Boxes indicate measured variables. Hexagons indicate a composite variable, pooling effects of four biocrust properties (inlaid within the hexagons). Arrows indicate a directed effect of one variable upon another, scaled proportionally to adjacent path coefficients. For graphical simplicity, effects of burrowing on the four biocrust properties are left out of the diagram. They are: d. burrowing → composition = 0.05, burrowing → cover = −0.25 (P = 0.02), burrowing → aggregation = 0.36 (P = 0.008), burrowing → composition = 0.23 (P = 0.04). e. burrowing → composition = 0.13, burrowing → cover = −0.28 (P = 0.02), burrowing → aggregation = 0.36 (P = 0.001), burrowing → heterogeneity = 0.20 (P = 0.08).

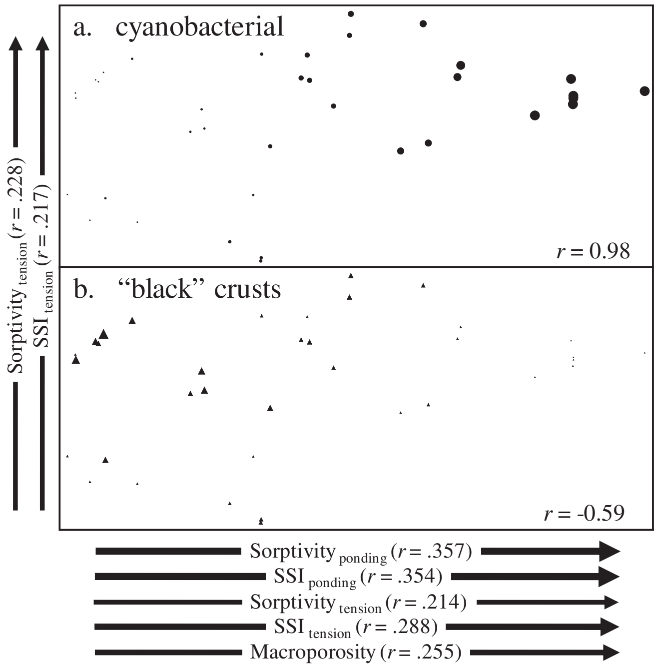

Fig. 3. NMDS ordination of biocrust composition on dunes. Upper and lower panels repeat the same configuration of points in ordination space with points scaled proportionally to the abundance of cyanobacterial (a) and "black" crusts (b). The ordination is rotated to maximize its correlation with $SSI_{ponding}$ on the horizontal axis. Correlations of other infiltration variables with ordination axes are also presented, along with arrows indicating the direction in which a given variable increases.

simulated infiltration rates by about 12–13% on dunes and about 16–17% on swales. Based on pit cover values post-reintroduction of bilbies (dune = 1.01%; swale = 1.37%), these rates all increased by another 2.3–2.5%.

When we modeled different scenarios for animal pits, both pre- and post- bilby reintroduction, only minor changes in probability of run-off yielding rainfall intensities were observed (Fig. 5); only at maximal foraging pit density (dune = 2.04%; swale = 2.09%) did

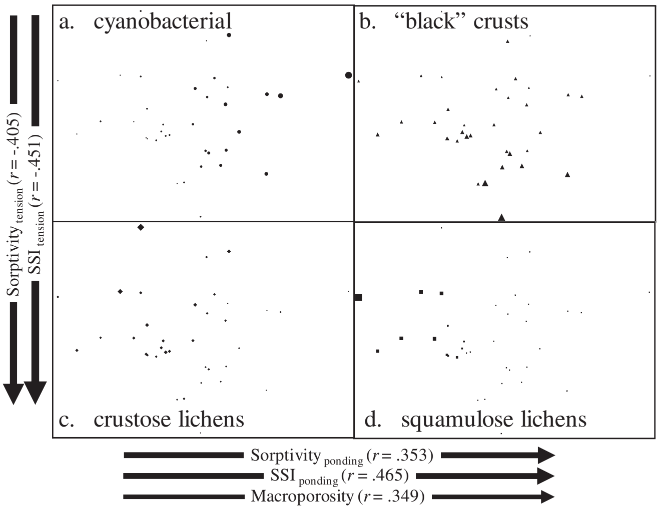

Fig. 4. NMDS ordination of biocrust composition on swales. Different panels repeat the same configuration of points in ordination space with points scaled proportionally to the abundance of cyanobacterial (a), "black" crusts (b), crustose lichens (c), and squamulose lichens (d). The ordination is rotated to maximize its correlation with $SSI_{ponding}$ on the horizontal axis. Correlations of other infiltration variables with ordination axes are also presented, along with arrows indicating the direction in which a given variable increases.

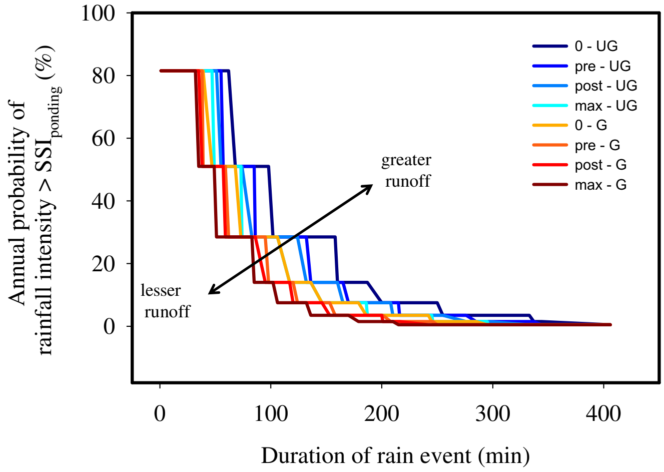

Fig. 5. Annual probability of occurrence of rainfall intensities greater than $SSI_{ponding}$ at varying event durations. Lines represent different scenarios of animal pit cover, each having its own $SSI_{ponding}$ value simulated using SEM equations derived here and unpublished field data on soil surface properties (Eldridge unpublished). Probabilities are derived from data given by the Government of Australia Bureau of Meteorology (http://www.bom.gov.au/hydro/has/cdirswebx/cdirswebx.shtml). 0 − UG = no burrows, ungrazed; pre − UG = pre-bilby burrow density, ungrazed; post − UG = post-bilby burrow density, ungrazed; 0 − UG = maximal burrow density, ungrazed; 0 − G = no burrows, grazed; pre − G = pre-bilby burrow density, grazed; post − G = post-bilby burrow density, grazed; max − G = maximal burrow density, grazed.

probabilities begin to diverge from the no burrow scenario ($P = 0.02$; Appendix 2 in Supplementary Material). Even when our scenario modeled the maximal animal pit cover observed at Scotia, a value more than double that of a similar environment with a long history of reintroduction (James et al., 2009), run-off yielding rainfall intensities were still very probable at a variety of event durations. When scenarios simulated grazing-linked reduction in biocrust cover and retardation of biocrust succession, it was clear that despite the strong microscale impacts of individual bilby burrows, surface disturbances with a greater areal extent such as those associated with grazing are much more likely to disrupt macroscale hydrological function. Probabilities of run-off events were about the same for the maximal bilby foraging pit – ungrazed and no bilby forage pit – grazed scenarios, but otherwise all grazed scenarios differed from all ungrazed scenarios ($P = 0.06$–<0.0001; Table 1). As in the ungrazed scenarios, the only difference attributable to bilby foraging was between the two burrowing extremes i.e. no foraging to maximal bilby foraging levels ($P = 0.04$; Table 1).

4. Discussion

Our design included two ecosystem engineers of major importance for patch-scale hydrology, as demonstrated by the fact that our models explained an important percentage of the variation in the different infiltration measurements. Our upscaling to dune-swale systems suggests that biocrusts may determine the ability of upslope dune crests to produce runoff and therefore overall productivity. The ability of the bilby, at realistic densities, to counter this function of biocrusts is detectable. However, it is a minor influence on hydrology compared with removal of biocrusts by livestock trampling, which is a much more widespread disturbance type.

4.1. Effects of bilbies and biocrusts in determining infiltration processes

Bilbies and biocrusts exert comparable and often opposite effects on various aspects of infiltration. Infiltration of water into soil regardless of pore size (under ponding) was under dual control of bilbies and biocrusts, whereas biocrusts but not bilbies determined infiltration through micropores alone (under tension; Table 1, Fig. 2). A portion of the effect that both engineers exerted upon infiltration under ponding may be explained by macroporosity, which was influenced most strongly by biocrusts, and to a lesser degree by bilbies (Table 1).

These effects of bilbies were essentially all direct effects (Table 1), meaning that the effects were not due to modification of biocrust properties. This could partly be because the correlation was diminished between bilby foraging pits and biocrust properties in our sampling strategy, as opposed to a purely random sampling strategy. Eldridge et al. (2010) employed a similar strategy to study the effects of rabbits and biocrusts on infiltration, and surprisingly found that rabbit effects were nearly all *indirect*, manifested through their alteration of biocrusts. Therefore, we do not believe that our sampling strategy is incapable of detecting indirect effects. Bilbies did in fact influence biocrust cover, spatial aggregation and heterogeneity, but because these were not the most important properties of biocrusts in terms of determining infiltration (*discussed below*), these indirect effects were minor.

What accounts for the different effect of rabbit and bilby burrows? In the Spanish case, the gypsum soils dug by rabbits were prone to sealing once the aggregate structure was disrupted. This does not occur in the present study (Table 1), possibly because both the dunes and the swales contain considerably more sand than the Spanish soil, which would make the soils less prone to sealing (Appendix 1). Another plausible mechanism might be enhanced macroporosity, which was detected in our models. The digging of the bilby may promote activity of invertebrate soil fauna, or conversely, bilbies may preferentially target high densities of macropores in their search for soil-dwelling fauna. Indeed, bilbies are known to forage for termites, beetles and soil-dwelling spiders (e.g. Lycosidae), which construct relatively large macropores in the soil (Spain et al., 1983) which can in turn conduct large volumes of water. Removal of the immediate surface layers will likely uncover invertebrate galleries and channels, providing connectivity to the subsurface (e.g. Eldridge, 1994). In contrast, rabbits dig to forage on the roots of annual plants, and their foraging pits are shallow and less likely to encounter root channels or invertebrate burrows.

When biocrusts were either more advanced in their successional state, or more abundant overall, they largely reduced infiltration in both the run-off generating dunes, where it is beneficial to ecosystem productivity, and in run-on catchments where enhancement of infiltration would benefit ecosystem productivity. The role of biocrusts in the run-off/infiltration balance has been somewhat controversial with many authors stating that biocrusts are run-off generators (Yair, 1990; Maestre et al., 2002; Wang et al., 2006; Fischer et al., 2009), and a smaller number of authors claiming that at least certain types of biocrusts promote infiltration (Brotherson and Rushforth, 1983; Harper and Marble, 1988; Greene et al., 1990; Eldridge et al., 2010). It is our opinion that this debate is largely fruitless, because there is not one answer to the question of whether biocrusts promote infiltration or run-off: they do both in different circumstances. Biocrusts differ strongly in composition and physical structure from place to place, and our results here and in Spain (Eldridge et al., 2010) and the results of other authors (Almog and Yair, 2007; Yair et al., 2008; Chamizo et al., 2011; Yair et al., 2011) suggest that composition might be as important or more important than crust abundance in determining the hydrological role. Macroscale properties such as surface roughness of biocrusts are also key differences among study areas (Belnap, 2006). The real challenge is not to finally answer whether biocrusts aid infiltration or not, a false dichotomy, but to find all of the relevant factors and parameterize the general model that predicts biocrust hydrological function around the world.

4.2. Relative influence of biocrust community properties on infiltration

Due to its variation on small scales (Fig. 1), the biocrust study system allows us to compare the relative influence of various community and micro-landscape properties in the determination of hydrological function: total cover, community composition, heterogeneity, and spatial aggregation (Bowker et al., 2010a,b; Maestre et al., 2012). All of these are known to exert effects on productivity (Kahmen et al., 2005), ecosystem function (Okin et al., 2009) or landscape function (Ludwig et al., 2007) in the literature, but are not often studied together to learn their relative importance (but see Maestre et al., 2005; Maestre and Escudero, 2009).

The most influential biocrust property was functional group composition, a variable convincingly more important than the total biocrust cover. We also found that composition was highly important in biocrust hydrological properties in Spain, though less so than cover (Eldridge et al., 2010). Different compositions had different effects on the dune and swale settings. On dunes, the longer biocrust succession is allowed to occur (from early successional cyanobacterial crusts to either “black” crusts, mosses or lichens), the better the dunes can function as run-off zones (Fig. 3). On swales, a more complex picture emerges. Different community properties maximize infiltration under tension and ponding (Fig. 4). Under ponding, when water infiltrates through both macro- and micropores, cyanobacterial crust dominance maximizes infiltration whereas squamulose lichen dominance retards it. Under tension, when water infiltrates only through micropores, “black” crusts are best associated with water capture while crustose lichens are more likely to generate run-off. In Spain, the clear compositional feature that determined biocrust promotion of infiltration was cover of mosses, as opposed to lichens, which promoted run-off (Eldridge et al., 2010). This generalization was also supported by Chamizo et al. (2011), also in Spain, though on two distinct soil types. Several studies (Almog and Yair, 2007; Yair et al., 2008, 2011) also suggest that in dune systems of Israel, moss vs. cyanobacterial dominance of biocrusts strongly influences hydrological functions of biocrusts. In the present study, the effect of mosses was neutral, possibly because the dominant mosses were short-statured. Taller mosses often exhibit subsurface stem tissue (Danin and Ganor, 1991), which upon decay could conceivably create vertical macropores up to centimeters in length.

The sole result of note pertaining to spatial biocrust characteristics was that under tension, greater heterogeneity decreased infiltration on dunes and increased infiltration on swales. Neither of these effects were clearly distinct from zero, but the two habitat types differed from each other. The promotion of infiltration by increasing small scale biocrust heterogeneity in swales may have more to do with the capture of mobile resources such as sand which might increase microporosity. Biocrust patches tend to be slightly raised compared to adjacent uncrusted patches, therefore a heterogeneous biocrust surface may accumulate materials. The situation on dunes is much different. It is uncommon for extensive, homogenous crust cover to develop on dunes. The more common type of homogeneous microsites on dunes are those where crust development is poor and the surface has a high proportion of unconsolidated sand. This is a result of the more exposed location, frequent disturbance by animals, which tend to forage in dune soils, and the brittle nature of the surface. This apparent reduction of infiltration with increasing heterogeneity may simply be due to the progression of biocrust succession, which creates heterogeneity.

Overall, our data seem to provide support for the assertion of Maestre et al. (2005) that spatial pattern is a weaker determinant/driver of ecosystem function than other community properties such as cover, evenness and richness. Holding total cover constant in experimentally constructed biocrusts, Maestre et al. (2012) found that species richness and composition exerted the greatest control over nutrient cycling. Spatial aggregation (or lack thereof) exerted some effects, and evenness was largely unimportant. Using naturally occurring biocrusts in the field, Bowker et al. (in press) found that biodiversity and total cover more often and more strongly affected nutrient cycling. But in the case of C-cycling, another component of spatial pattern – the patch-size distribution – was also influential.

4.3. Does bilby reintroduction reduce macro-landscape function?

Hydrological ecosystem function in these dune-swale macro-landscapes relies upon export of run-off from dunes and its subsequent capture in swales. We found that the same forces governed infiltration in run-on and run-off zones; although actual infiltration rates differ considerably. Dunes and swales differ in function owing to slope and landscape position: run-off zones are sloped and positioned above relatively flat run-on zones. Because swales are flat, energy of run-off is low thus they may capture run-off regardless of their surface characteristics. This capture would be maximized if swale biocrusts were in an early successional cyanobacterial state, however this scenario could present tradeoffs in wind erosion susceptibility (Belnap and Gillette, 1998) and soil fertility (Dougill and Thomas, 2004; Houseman et al., 2006; Delgado-Baquerizo et al., 2010). Dunes and swales also differ in prevalence of animal burrows, including those of the bilby. Bilbies were previously documented to preferentially forage on dunes and dune-swale ecotones rather than hardpan swales (James and Eldridge, 2007), however in the Scotia Sanctuary, swales have had about 30% more animal burrow cover in the 2 years since the reintroduction (Eldridge et al., 2012). These forage pits enhance soil fertility and capture resources such as seeds, litter and fungal spores and therefore promote ecosystem productivity (Eldridge and James, 2009; Travers et al., 2012). These are likely positive influences on ecosystem function but their possible disruption of run-off generation must also be taken into account. Despite that they are common and that they may be equally or more influential than biocrusts in the micro-scale redirection of water, the actual cover of bilby foraging pits was small on the landscape (usually less than 1% cover; James and Eldridge, 2007; Eldridge et al., 2012).

Our model extrapolations indicate that an unrealistically high density of ground-foraging animal pits would be required to break down the hydrological function of the macro-landscape, whereas a hypothetical stressor which removes biocrusts – such as livestock trampling – could easily lead to deviations in the hydrological regime of these patterned landscapes. Of course, livestock use is much more complicated than our simple model projection, and may lead to changes in the productivity and spatial patterning of vegetation, soil erosion and soil compaction on less sandy soils (Graetz and Tongway, 1986; Yates et al., 2000). Our model focuses solely on what would likely be the most immediate grazing impact: the loss of biocrusts. Since our models explain less than half of the variation in our data (Table 1), these extrapolations are only approximations of the direction and magnitude of change. Despite these caveats we can confidently conclude that the conservation of the endangered bilby and all of the benefits to ecosystem function associated with co-location of mobile resources such as water, seeds and litter in bilby foraging pits (Eldridge and James, 2009; Travers et al., 2012) need not come at the cost of hydrological function at the landscape scale. This conclusion is only strengthened when the comparatively trivial impacts of bilby foraging pits to local hydrology are compared to a rather conservative estimate of livestock grazing impacts that are currently underway throughout Australia.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2013.02.002.

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