

# Interactive Effects of Three Ecosystem Engineers on Infiltration in a Semi-Arid Mediterranean Grassland

David J. Eldridge,<sup>1\*</sup> Matthew A. Bowker,<sup>2</sup> Fernando T. Maestre,<sup>2</sup> Patricia Alonso,<sup>2</sup> Rebecca L. Mau,<sup>2</sup> Jorge Papadopoulos,<sup>2</sup> and Adrián Escudero<sup>2</sup>

<sup>1</sup>Ecology and Evolution Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia; <sup>2</sup>Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, 28933 Móstoles, Spain

## ABSTRACT

The redistribution of water in semi-arid environments is critical for the maintenance and survival of vegetation patches. We used a systems approach to examine the interactive effects of three engineers—*Stipa tenacissima*, biological soil crusts, and the European rabbit (*Oryctolagus cuniculus*)—on infiltration processes in a model gypseous semi-arid Mediterranean grassland. We measured the early (sorptivity) and later (steady-state infiltration) stages of infiltration at two supply potentials using disk permeameters, which allowed us to determine the relative effects of different engineers and soil micropores on water flow through large

macropores. We detected few effects under tension when flow was restricted to matrix pores, but under ponding, sorptivity and steady-state infiltration adjacent to *Stipa* tussocks were 2–3 times higher than in intact or rabbit-disturbed biological soil crusts. Structural Equation Modeling (SEM) showed that both *Stipa* and biological soil crust cover exerted substantial and equal positive effects on infiltration under ponding, whereas indirectly, rabbit disturbance negatively affected infiltration by reducing crust cover. Under tension, when macropores were prevented from conducting water, *Stipa* had a direct negative effect and biological soil crust cover was relatively unimportant. More complex SEM models demonstrated that (1) *Stipa* primarily influenced biological soil crusts by reducing their richness, (2) rabbits exerted a small negative effect on crust richness, and (3) lichens were negatively, and mosses positively, correlated with a derived “infiltration” axis. Our results highlight the importance of biological soil crusts as key players in the maintenance of infiltration processes in *Stipa* grasslands, and demonstrate the modulating role played by rabbits through their surface disturbances.

**Key words:** infiltration; *Oryctolagus cuniculus*; biological soil crust; ecosystem engineering; macropore; *Stipa tenacissima*; ponding; permeameter.

Received 14 February 2010; accepted 16 April 2010;  
published online 11 May 2010

**Electronic supplementary material:** The online version of this article (doi:10.1007/s10021-010-9335-4) contains supplementary material, which is available to authorized users.

**Author Contributions:** DJE, MAB, FTM conceived the study; AE contributed original ideas; DJE, MAB, PA, RLM, JP performed the research; DJE, MAB analyzed the data and wrote the paper.

\*Corresponding author; e-mail: d.eldridge@unsw.edu.au

## INTRODUCTION

Water is a strong driver of ecosystem function, productivity, and diversity in arid and semi-arid ecosystems (López-Portillo and Montaña 1999). Water availability varies profoundly in space and through time, and consequently, soil moisture has a patchy distribution, varying across entire catchments or watersheds at landscape scales to individual plants or groups of plants at small spatial scales (for example, Bochet and others 1999). The distribution and redistribution of water in turn influences patterns of vegetation, which in many areas, is tightly controlled by deposition processes from areas upslope, and through complex interactions between individual plants and biotic and abiotic components of the interspaces (Puigdefábregas and Sanchez 1996; Cerdá 1997; Bochet and others 1999; Eldridge and others 2002). In addition, water distribution and redistribution may be affected by physical habitat alterations of ecosystem engineers (Jones and others 1994).

A wide range of biota has demonstrated effects on infiltration processes across broad spatial scales in both temperate and mesic environments. The roots and stems of trees and shrubs enhance infiltration directly by altering soil porosity (Dunkerley 2000; Bhark and Small 2003). Infiltration under woody plant canopies can be moderated by livestock or native animal disturbance when the soil surface is disrupted during camping or habitat construction (Dean and Milton 1991; Kerley and others 2004). Macro-invertebrate burrows and channels close to the stems of woody plants enhance infiltration close to the roots, reinforcing the higher levels of infiltration typically found under plant canopies. In higher rainfall areas, wind throw and tree fall alter water flows by increasing surface ponding and disrupting soil macropores (Mitchell 1988; Wilkinson and others 2009) and potentially increasing accessions of water to the water table (Bardgett and other 2001).

Fauna such as rodents and rabbits influence infiltration processes by disrupting soil surface horizons, altering the placement and decomposition of litter, thereby influencing hydrophobicity and subsoil permeability (for example, Mitchell 1988; Whitford and Kay 1999). Colonial (for example, ants and termites) and solitary (for example, cicadas, crickets, earthworms) meso-fauna create macropores that form linkages to the subsurface, and may be important for maintaining continuity of flow between terrestrial and aquatic ecosystems (Bardgett and others 2001). Similarly, incorporation of organic matter and nutrient-rich

caste material by earthworms into soil has substantial effects on soil physical properties (Jégou and others 2001). Finally, the activities of microbes and soil meso-fauna can alter the quantity and decomposition of litter and soil nutrient levels, which are linked directly to soil physical properties such as soil porosity and therefore infiltration processes (Lavelle and others 1997; Bardgett and others 2001).

In arid environments, a number of ecosystem engineers have demonstrated substantial influences on ecosystem properties and processes through their effects at the soil surface. These effects include physical resource engineering by all-genic ecosystem engineers (organisms whose activities physically modify the availability of resources or living space for other organisms *sensu* Jones and others 1994) such as semi-fossorial animals, whose foraging activities decrease soil aggregation, alter pore size distribution, but may provide entry points for water to infiltrate (for example, Myers and others 1994; James and others 2009). Similarly, autogenic engineers—those whose physical structures have an effect on the environment and resource availability for other organisms (*sensu* Jones and others 1994)—such as woody plants and grasses enhance infiltration through the creation of macropores and biovoids in the soil (Bhark and Small 2003), and non-vascular engineers such as mosses and lichens forming biological soil crusts influence runoff and erosion processes at smaller spatial scales (Eldridge and others 2000; Maestre and others 2002). Many of these infiltration processes are moderated by grazing (Whitford 1996). Surface disturbance by livestock, however, can moderate these effects and reduce infiltration by destroying soil aggregates, reducing macroporosity and disrupting macropore continuity to the surface (Eldridge and Freudenberger 2005). Although examples of single engineer effects on ecosystem function from arid systems have been widely reported in the literature (for example, Wesche and others 2007), we are unaware of any studies that have specifically examined the combined and interactive effects of a spectrum of engineers, as diverse in form and function as vascular plants, non-vascular (biological soil crust) organisms, and vertebrates.

Here we report on a study of the interactive effects of three such engineers on the source–sink nature of water infiltration in a semi-arid gypsumiferous Mediterranean grassland: (1) the dominant tussock grass *Stipa tenacissima* L., which is a sink for water, and primarily an autogenic ecosystem

engineer, (2) biological soil crusts which are primarily autogenic ecosystem engineers, and in similar environments function as a source of water by enhancing runoff processes, and (3) European rabbits (*Oryctolagus cuniculus* L.), which are allogenic ecosystem engineers whose activity enhances sink strength in impacted microsites. In addition to having additive effects upon infiltration, these ecosystem engineers can potentially influence each other's effects on the environment, requiring a system approach.

We advanced the following conceptual model outlining the major players in our study system and their interactions. The predominant sinks for water in arid and semi-arid Mediterranean grasslands are large *Stipa tenacissima* tussocks (Puigdefábregas and others 1999). Given their size and degree of root penetration into surrounding soils, these tussocks behave functionally more like trees and shrubs than grasses, and therefore act as 'ecosystem wicks' (*sensu* Eldridge and Freudenberger 2005). *Stipa* tussock sinks often derive water and sediment from upslope source areas that often support a variable cover of biological soil crusts, complex associations of cyanobacteria, lichens, and bryophytes (Maestre and others 2002; Maestre and Cortina 2003). Biological soil crusts create zones of water repellency and either singly or as an aggregated community, redirect runoff water downslope (Maestre and Cortina 2002; Maestre and others 2002), often into *Stipa* tussocks. Biological soil crust organisms may also physically impede soil pores at the soil surface, further retarding infiltration and increasing runoff. Soil disturbance caused by rabbit digging physically reduces the cover and therefore activity of surface crusts, and their pits could conceivably enhance the capture and retention of water (James and others 2009). Given their large size, *Stipa* tussocks create surface shading in a considerable area around their base (Maestre and others 2001). This likely alters the community of biological soil crust organisms by favoring shade-tolerant species and influences the behavior of rabbits seeking resting sites.

We provide an empirical test of this model to help develop an understanding of how an ecosystem function arises due to a complex system dominated by tri-partite ecosystem engineering. Specifically, our goals were to: (1) estimate the relative contributions of three engineers upon infiltration processes, (2) partition direct and indirect effects of two of the engineers, and (3) determine which community properties of biological soil crusts are most relevant to infiltration processes, and how they are affected by the presence of *Stipa* tussocks and the activity of rabbits. A system-based

understanding of infiltration can serve as a foundation for improved dryland ecosystem management for often-competing social outcomes such as maintaining productivity of grazing and hunting lands, water conservation, and naturally based flood control.

## MATERIALS AND METHODS

### Site Description

This research was conducted in the Aranjuez Experimental Station, in the center of the Iberian Peninsula (40°02' N–3°37' W; 590 m a.s.l.; 8° slope, Figure 1). The climate is Mediterranean semi-arid, with a 30-year average rainfall and temperature of 388 mm and 13.8°C, respectively. There is a pronounced dry season from June to September, with only small amounts of rain. The soil is derived from gypsum outcrops, and is classified as Xeric Haplogypsid (Soil Survey Staff 1994). It supports a biological soil crust community dominated by lichens such as *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (Weber) Poelt, *Fulgensia subbracteata* (Nyl.) Poelt, *Toninia sedifolia* (Scop.) Timdal, and *Psora decipiens* (Hedw.) Hoffm. (~34% cover) and mosses such as *Didymodon* sp. The vascular vegetation is an open grassland dominated by *Stipa tenacissima* (~18% cover), with scattered *Retama sphaerocarpa* (L.) Boiss., *Helianthemum squamatum* (L.) Dum. Cours, and *Thymus* spp. shrubs. The area is used by hunters and supports a high density of rabbits that are maintained by supplementary water and grain for hunting. When undisturbed by these animals, the soil surface under the canopy of *Stipa* tussocks has a well-developed biological soil crust dominated by mosses, principally *Pleurochaete squarrosa* (Brid.) Lindb.

### Infiltration Measurements

We measured two 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.

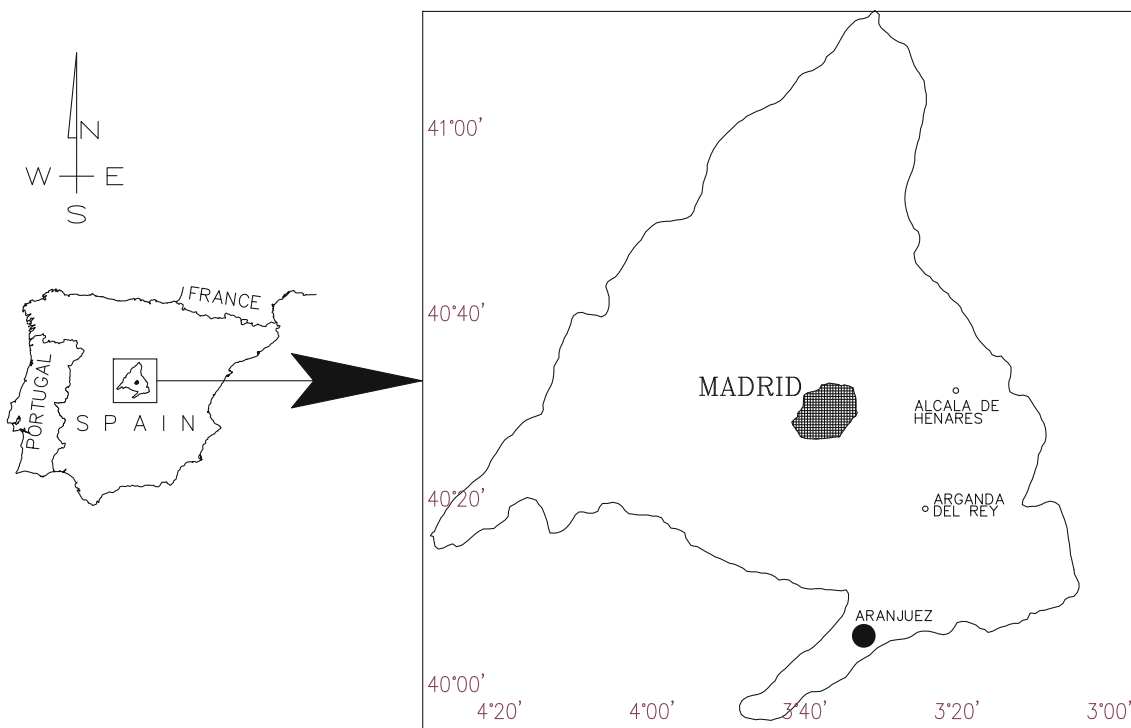


Figure 1. Location of the Aranjuez experimental station within the Iberian Peninsula.

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 (ponding), sorptivity (tension), steady-state (ponding), and steady-state (tension). Interpretation of the difference between measurements under ponding and tension rely upon the distinction between matrix pores (*syn.* micropores) and macropores. Matrix pores occur between individual mineral grains and between soil particles, and are 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 fifth 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 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 healthy, highly conductive soils, and soils with a high biological activity or large macroarthropod populations will have a high ratio (White 1988). A loss of ecosystem function in terms of water flow, can be attributed, in a large part, to a loss of this macroporosity.

Water flow was measured at 60 locations on a slightly north-facing slope over an area of approximately  $3$  ha. Thirty locations were adjacent to, and upslope of, large *Stipa* tussocks, and 30 were in the interspaces, more than about  $2$  m from *Stipa* tussocks. For both the 30 *Stipa* and 30 interspace locations, we non-randomly selected sampling locations representing the entire possible gradient of biological soil crust cover, rabbit disturbance, and undisturbed bare ground. To ensure that we captured the extremes of this gradient, we first selected five each of plots with greater than 90% biological crust cover, rabbit disturbance, and undisturbed bare ground. The remainder represented a variety of different combinations of these three ground cover components. This non-random

design is ideal for discerning the relative importance of direct effects of rabbits, biological soil crusts or *Stipa* upon infiltration, while decreasing correlation among these players as much as possible in a non-experimental setting. At every location where biological soil crust was recorded, we estimated the cover of all crust species within the same circular ring (see below) used to set up the permeameters.

For water flow measurements, both ponded and unsaturated permeameters were placed about 70 cm apart. The unsaturated permeameter was placed on a thin bed of sand to provide a uniform contact with the soil surface and the ponded permeameter placed on a steel ring and sealed along the outside edge to prevent leakage of water. The permeameters were run until steady-state had been achieved (15–30 min). At each supply potential, sorptivity was calculated according to the method of Cook and Broeren (1994), and steady-state infiltration according to White (1988).

## Statistical Analyses

We conducted a two-phase analysis of the data. The purpose of the first phase was to estimate the relative importance of the various ecosystem engineers on infiltration, and to evaluate the relative magnitude of their multiple pathways of influence. The second phase involved a more detailed assessment of the interactions among the engineers and biological soil crust composition.

In Phase I we undertook two complementary analyses: (i) a two-way ANOVA approach using only data for the five plots where the surface over which infiltration was being measured was completely disturbed by rabbit digging or occupied by 100% biological soil crust cover for each of the *Stipa* and interspace samples ( $n = 20$ ) to provide an easily understandable summary of the maximal effects of the engineers upon infiltration, and (ii) a structural equation modeling (SEM) approach to analyze our data as a system of variables, and partition multiple effects of ecosystem engineers upon infiltration variables (Grace 2006). We initiated the process by advancing an *a priori* model of our system, wherein biological soil crust cover, rabbit disturbance and presence of *Stipa* all had direct effects upon infiltration response variables. Further, *Stipa* was proposed to influence infiltration indirectly by influencing crust cover and rabbit disturbance. Finally, rabbits were proposed to influence infiltration indirectly by decreasing cover. To improve normality, we log-transformed all of the infiltration response variables prior to

analysis. We used Akaike's Information Criterion (AIC) to select among a set of six nested models of varying complexity reduced from this global model (Burnham and Anderson 2002). This procedure was repeated for each of the five infiltration response variables, and the model with the lowest AIC value in each set was selected as the best model (Appendix 1 in Supplementary material). This approach allows a *relative* assessment of models in a set, but does not tell us about the absolute quality of a model. To obtain information about the absolute fit of the best model, we estimated path coefficients and performed associated probability tests for the best model in each set and performed overall goodness of fit tests. The goodness of fit test estimates the probability that the data deviate from the model structure, thus high probability values indicate that these models are highly plausible causal structures underlying the observed correlations.

The SEM analysis for Phase II was restricted to those locations where biological soil crust cover was greater than 0% ( $n = 43$ ). Of the three engineers, this crust is the most complex because, unlike *Stipa* and the European rabbit, it represents a diverse community of organisms. At every location where a biological crust was recorded we calculated richness and a measure of community composition based on community proportional abundance data from a non-metric MDS (nMDS) ordination (McCune and Mefford 2004). The proportional transformation purges information on total cover in the sample, and therefore reflects community composition and relative abundance of various species. The ordination was rotated to maximize correlation with infiltration under ponding, and the axis that corresponded to infiltration was extracted. The Phase II analyses allowed us to determine the relative influence of various crust community attributes on infiltration, and to seek to understand which attributes are being controlled to some extent by other engineers.

## RESULTS

### Phase I—ANOVA Analyses

Sorptivity under tension was higher in the interspaces than adjacent to *Stipa* tussocks ( $F_{1,16} = 6.12$ ,  $P = 0.025$ ; Figure 2A), but there was no difference between crusted and rabbit disturbed sites (Figure 2B). There were no differences, however, in steady-state infiltration under tension between *Stipa* and interspace soil, or between crusted and rabbit disturbed soil. In general, water flow effects

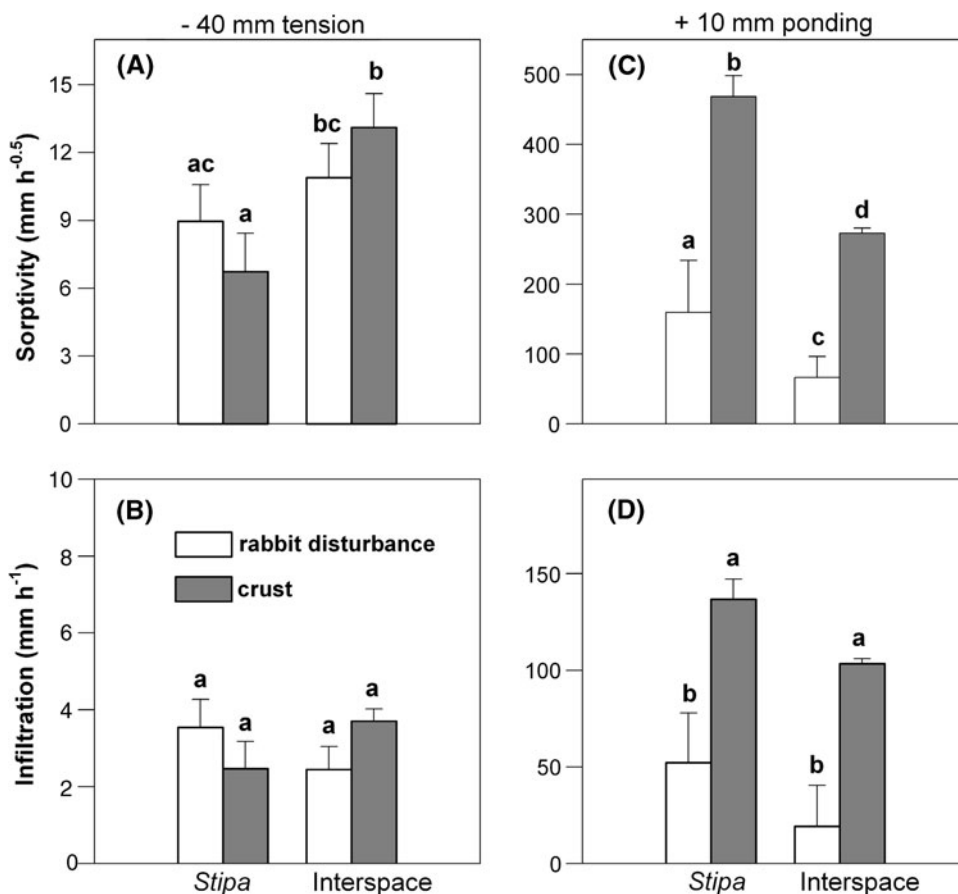


Figure 2. Mean ( $\pm$ SE,  $n = 20$ ) sorptivity and steady-state infiltration under tension (A, B) and ponding (C, D) for rabbit disturbances and undisturbed biological soil crusts adjacent to *Stipa tenacissima* tussocks and in the interspace areas located between them. Different letters within a graph indicate a significant difference in means at  $P < 0.05$ ; Tukey's HSD.

were most apparent under ponding when flow was predominantly macropore-driven. Pondered sorptivity adjacent to *Stipa* tussocks ( $314 \text{ mm h}^{-0.5}$ ) was almost double that in the interspace soils ( $170 \text{ mm h}^{-0.5}$ ;  $F_{1,16} = 11.34$ ,  $P = 0.004$ ), whereas sorptivity through biological soil crusts was more than three-times that through rabbit-disturbed soil ( $370$  compared to  $113 \text{ mm h}^{-0.5}$ ;  $F_{1,16} = 36.0$ ,  $P < 0.001$ ; Figure 2C). Trends were similar at steady-state, where infiltration was 1.5-times greater under *Stipa* tussocks ( $F_{1,16} = 11.43$ ,  $P = 0.004$  on  $\log_{10}$ -transformed data) and 3.4-times greater through the biological soil crust than through rabbit disturbed soils ( $F_{1,16} = 47.8$ ,  $P < 0.001$ ; Figure 2D). The macropore ratio, the ratio of sorptivity under ponding to that under tension, which provides an index of the relative importance of macropores in the infiltration process, was greater adjacent to *Stipa* (66:1) than in the interspaces (14:1;  $F_{1,16} = 17.79$ ,  $P = 0.001$  on  $\log_{10}$ -transformed data).

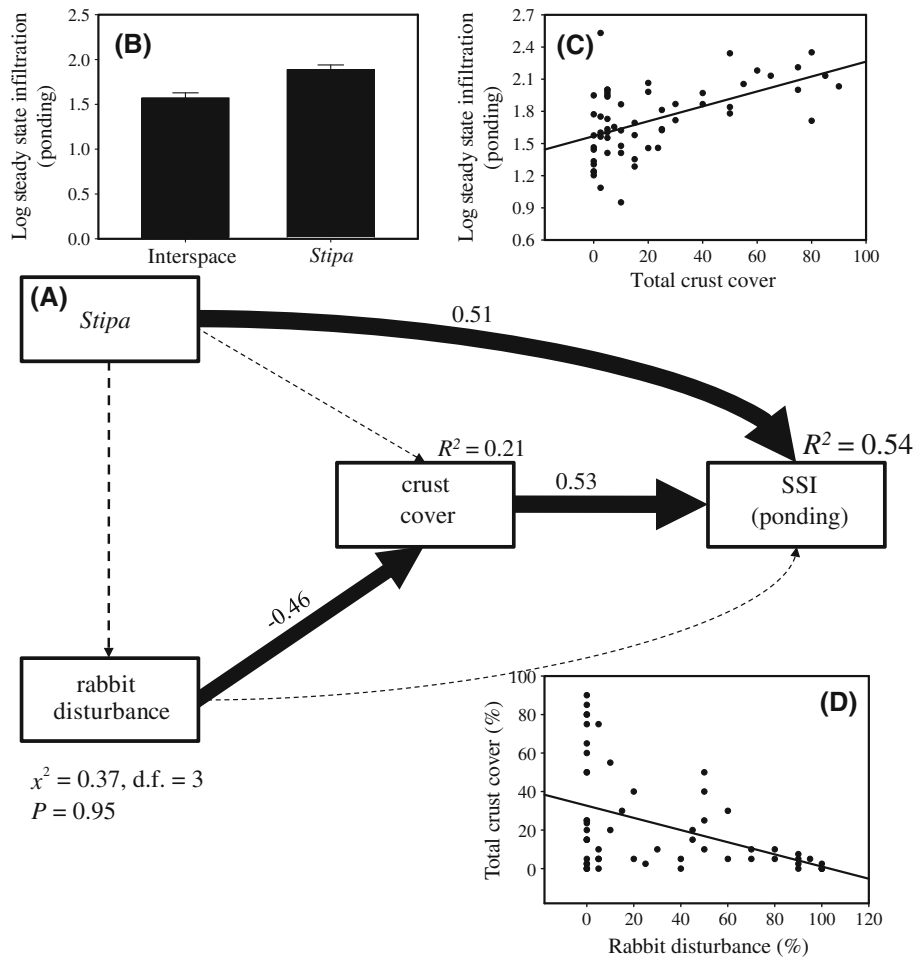
### Phase I—Structural Equation Modeling

In all model sets evaluated, the best model selected was the seven parameter model which eliminates the

effect of *Stipa* on biological soil crust cover and rabbit disturbance, and the direct effect of rabbits on infiltration (Appendix 1 in Supplementary material). The best model for steady-state infiltration (Figure 3) indicated that *Stipa* and biological soil crust cover exerted an approximately equal effect on infiltration, explaining greater than half of the variance. Rabbit disturbance had a similarly strong negative effect on biological soil crust cover ( $-0.46$ ), but no direct effect on infiltration. The remaining models had the same form (Table 1). Though the path coefficient estimates differed slightly, the models for sorptivity under ponding and the macropore ratio were similar. In contrast, the models for infiltration parameters under tension left much more variance unexplained ( $R^2 \leq 0.13$ ), as crust cover was not an important factor. For sorptivity under tension, the presence of *Stipa* actually had a moderate direct and negative effect ( $-0.35$ ). All models exhibited excellent absolute goodness of fit ( $\chi^2 \leq 0.14$ ;  $P \geq 0.67$ ).

### Phase II

Ordination of data on community composition and relative abundance of crust taxa indicated that in general, lichens were negatively correlated with



**Figure 3.** Effects of three interacting ecosystem engineers upon infiltration. **A** Final structural equation model illustrating ecosystem engineer effects upon steady-state infiltration under ponding. Boxes represent variables measured in the study, and arrows represent influences exerted by one variable upon another. Path coefficients (ranging from 0 to 1, and related to the partial correlation coefficient) appear adjacent to arrows. Arrow width is scaled proportionally to its corresponding coefficient. Dashed arrows are those present in the global model, but not in the best model (see Appendix 1 in Supplementary material). Statistics in lower left corner indicate satisfactory fit of the model. **B** Effects of *Stipa* on steady-state infiltration under ponding. **C** Effects of crust cover on steady-state infiltration under ponding. **D** Effects of rabbit disturbance upon total crust cover.

the derived “infiltration” axis whereas most mosses were positively correlated with it (Table 2).

The Phase II model (Figure 4) confirmed the direct effects of both *Stipa* and crust cover on steady-state infiltration under tension, and the effects of rabbits on biological soil crust cover. This model differed from the simpler Phase I model, which excluded information on crust composition, abundance, and structure. The biological crust cover effect was slightly weaker because the model included additional covarying crust properties. The ordination axis variable (a measure of crust community composition) also had a substantial effect, and richness had a small but not negligible effect. In this more complex model, *Stipa* primarily

influenced biological crusts by reducing their richness (*Stipa* shade results in *Pleurochaete* dominance). Rabbits also exerted a moderate effect on crust richness ( $-0.32$ ).

## DISCUSSION

Our study system is composed of the interactions among three ecosystem engineers, and their additive effects in influencing infiltration parameters. At the focal scale we found that both *Stipa* tussocks and biological soil crusts promoted infiltration, whereas rabbits compromised the crust effect. Our system is hierarchical (Allen and Starr 1982), and at lower levels of observation there exists at least

**Table 1.** Path Coefficients and Goodness of Fit Tests for the Four Remaining Best Models

Response variable	<i>Stipa</i> to infiltration	Crust to infiltration	Rabbit to crust	R <sup>2</sup>	χ <sup>2</sup>	df	P
Sorptivity under ponding	0.52***	0.52***	-0.46***	0.56	1.40	3	0.67
Sorptivity under tension	-0.35***	-0.06	-0.46***	0.13	0.06	3	0.90
Infiltration under tension	-0.20	0.05	-0.46***	0.04	0.45	3	0.93
Macropore ratio	0.56***	0.43***	-0.46***	0.50	1.40	3	0.70

Each row represents a best model containing the response listed in the leftmost column as the infiltration variable. Otherwise the model structure is identical to that in Figure 2, but the path coefficient estimates differ for each model. The next three columns list the path coefficients corresponding to the three paths in the models. Asterisks reflect probabilities that the path coefficients are equal to zero; \*\*\*P < 0.001. R<sup>2</sup> is proportion of variance explained in the infiltration variable listed on the left. χ<sup>2</sup>, df, and P are the test statistic, degrees of freedom, and probability value for the maximum likelihood χ<sup>2</sup> goodness of fit test; higher P-values indicate support for the model. All tests reported here indicate excellent fit.

**Table 2.** Pearson Correlations Between Individual Crust Taxa and an Axis of a Non-metric MDS (nMDS) Ordination Obtained from Biological Soil Crust Abundance Data

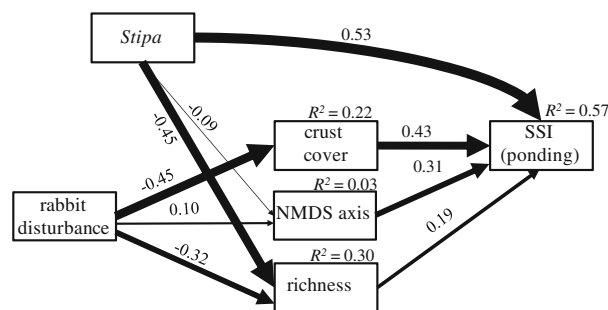
Taxon	Type	r
<i>Nostoc commune</i>	Cyanobacterium	-0.148
<i>Acarospora reagens</i>	Lichen	-0.315
<i>Buellia zoharii</i>	Lichen	-0.254
<i>Cladonia convoluta</i>	Lichen	-0.362
<i>Collema crispum</i>	Lichen	-0.104
<i>Disploschistes diacapsis</i>	Lichen	-0.419
<i>Fulgensia subbracteata</i>	Lichen	-0.615
<i>Psora decipiens</i>	Lichen	-0.498
<i>Squamarina cartilagenia</i>	Lichen	-0.206
<i>Squamarina lentigera</i>	Lichen	-0.431
<i>Tortula revolvens</i>	Moss	-0.278
<i>Didymodon</i> sp.	Moss	0.159
<i>Pleurochaete squarrosa</i>	Moss	0.610
<i>Syntrichia ruralis</i>	Moss	0.537
<i>Weissia</i> sp.	Moss	0.055

The ordination was rotated to maximize correlation with steady-state infiltration under ponding.

two key subsystems nested within this system. One subsystem is the unmeasured microfaunal community which likely generates macroporosity. The other is the biological soil crust community structure which can generate either runoff or infiltration, depending on which species prevail.

### The Effects of Three Ecosystem Engineers on Macroporosity

It is no surprise to find that *Stipa tenacissima* is a major sink for water in Mediterranean grass steppes, as a number of studies have previously reported greater levels of infiltration in *Stipa tenacissima* tussocks (Cerdá 1997; Maestre and others 2002). Our observations are consistent with results



**Figure 4.** Effects of three interacting ecosystem engineers upon infiltration and the relative effects of biological soil crust cover, composition (the nMDS axis) and richness on steady state infiltration under ponding.

from other arid areas showing substantial infiltration under both shrubs and grasses (for example, Scholte 1989; Nicolau and others 1996; Dunkerley 2000; Maestre and others 2002; Casmereiro and others 2003), and enhance our understanding of the importance of large, autogenic ecosystem engineers such as *Stipa* in enhancing water flow. Although various suggestions have been advanced to account for these *Stipa*-mediated effects ranging from upslope accumulation of sediment, to improved soil porosity (Puigdefábregas and others 1999), a clear demonstration of the underlying mechanism has been lacking. Our study unequivocally demonstrates the central role played by macropores in the dramatic positive effect of *Stipa* on infiltration. The macropore ratio was effectively about four-times greater next to *Stipa* than in the interspaces, confirming the overriding importance of macropores in creating a dichotomy between these ground surface types. The strong positive effect of shrubs on infiltration processes provides one mechanism for the persistence of the fertile island effect in water-limited environments (for example, Parsons and others 2003), and suggests that it may be partially mediated by yet another group which functions collectively as ecosystem engineers:



burrowing arthropods and other microfauna. *Stipa tenacissima* is known to initiate leaf growth in response to rain storms, even in summer (Pugnaire and others 1996). The extent to which summer growth translates into increased root growth and therefore enhanced porosity is largely unknown. Some macropores would have a high seasonal turnover, particularly those created by invertebrates that emerge in response to rainfall from burrows and emergence tunnels, particularly where they have a low structural integrity under summer storms.

Our data show a strong indirect negative effect of rabbits mediated by reduced biological soil crust cover but only weak direct effects of rabbit disturbance on infiltration (Figure 3; Table 1). This effect of rabbits on infiltration was strongest under ponding (Figure 3, Table 1). Under tension, however, rabbits had little effect on sorptivity or steady-state infiltration, suggesting that the effect of rabbit disturbance, even in the uppermost soil layers, is to alter macropore flow. Rabbit dung hills and latrines in the Iberian Peninsula have been shown to support active populations of dung beetles (*Thorectes valencianus*; Verdú and others 2009), increasing soil macroporosity through their dung burying activities and potentially enhancing infiltration. Overall, the present work on the effects of rabbits on infiltration processes suggests that similar mechanisms and responses are likely where rabbits and biological soil crusts coexist.

Like plants, biological soil crusts are known to support a rich suite of both micro- and macroarthropods (for example, Shepherd and others 2002), and may function as primary producers in food webs composed of microfauna (Neher and others 2009). They would also be expected to enhance or maintain macropore flow at the near surface layers by increasing the structural integrity of the macropore entrances (Herschel 1998; Zaady and Bouskela 2002). Rabbits typically construct shallow bedding sites or foraging pits that are less than 10 cm deep (D.J. Eldridge, unpublished data) which could disrupt the continuity of macropores to the subsoil, with mixed effects. Although this would initially increase water flow by exposing macropores to surface flows, the medium- to long-term effects would be to reduce water flow as the integrity of macropore necks breaks down in the absence of structural elements such as polysaccharides in the biological crust. Thus, it seems that a large degree of the apparent effects of the three types of engineers examined here may actually be mediated by facilitating, inhibiting, or nullifying the effects of soil microfauna.

## Biological Soil Crust Effects on Infiltration Depend Upon Community Structure

Unlike most arid sites studied where biological crusts tend toward hydrophobicity and enhance rather than reduce runoff (Alexander and Calvo 1990; Kidron and Yair 1997; Cantón and others 2002; Eldridge and others 2002), the crusts at this site appear to facilitate some degree of infiltration in the interspaces rather than solely redirecting water into plant canopies (Figure 3). This has been an area of much controversy, because it depends strongly upon the scale of observation, soil characteristics, the physical microtopography of biological crusts, and the dominant organisms of this crust. Studies from North American cold deserts and steppes have tended to suggest either little effect of these crusts, or an enhancement of infiltration, although many studies compare intact crusted areas with disturbed areas, making it difficult to separate biological soil crusts and disturbance effects (see Warren and Eldridge 2001 and references therein). Proposed mechanisms include a rugose microtopography at larger spatial scales, which slows overland flow resulting in eventual infiltration (Brotherson and Rushforth 1983; Warren and Eldridge 2001), or lessened detachment of fine particles during rainfall, which could seal surface pores (Loope and Gifford 1972).

In our model, total biological crust cover (+0.43) had the strongest effects on steady-state infiltration under tension (and other measures of infiltration), but both variables describing the community structure, especially the nMDS axis (+0.31), were also positively associated with infiltration. Enhanced microtopography or improved soil stability could be mechanisms underlying the crust cover effect, but the importance of community structure leads us to propose additional mechanisms: (1) biological soil crust community structure influences soil microfaunal activity, (2) various crust species are hydrophobic and hydrophilic, (3) heterogeneity in hydrophobic and hydrophilic surfaces may control micro-scale source-sink relationships. To our knowledge, our model shows for the first time the relationship between crust species-level community structure and ecosystem function in the form of infiltration, in a manner that allows the partitioning of its effects from other correlated factors. This work clearly demonstrates one reason why biological soil crusts behave differently at locations with different suites of components, as every lichen species is negatively

associated with infiltration, whereas four of five moss species are positively correlated with infiltration (Table 2).

Species composition of at least some groups of soil fauna tracks that of biological soil crusts (Darby and others 2007; Neher and others 2009). It is therefore conceivable that moss-dominated crusts support greater activity of burrowing microfauna. Another explanation may lie in physical properties of the mosses themselves. The water holding capacity of mosses can be impressive. In North American shrub steppes, *Syntrichia ruralis* can rapidly rehydrate after rainfall and store considerable volumes ( $\sim 14 \text{ l m}^{-2}$ ) of water (Eldridge and Rosentreter 2004). *Pleurochaete squarrosa*, which co-occurs with *Syntrichia* in our study site and often forms large patches under *Stipa*, attains even greater biomass per area, and therefore even greater water holding capacity. These two species are the strongest positive correlates with infiltration in our data, in contrast with the lichens *Fulgensia subbracteata*, *Squamarina lentigera*, and *Diploschistes diacapsis*, which slow infiltration rates proportionally as they become more abundant. Some studies have demonstrated different infiltration rates on contrasting homogenous biological crust types (for example, moss-dominated, cyanobacteria-dominated, and so on; Brotherson and Rushforth 1983; Eldridge and others 2000; Maestre and others 2002) but stopped short of treating community structure as a continuous variable in heterogeneous biological crusts composed of various combinations of species (Brotherson and Rushforth 1983; Eldridge and others 2000).

A final mechanism by which biological soil crust community structure could influence infiltration rates, is by generating heterogeneity in hydrophobic and hydrophilic patches. Biological soil crust communities are spatially discontinuous and, although supporting patches of hydrophobic crustose lichens such as *Diploschistes diacapsis* (Cantón and others 2004), contain many small gaps, even at the scale of the permeameter, which would act as micro-sinks for water. Infiltration in these micro-sinks could be enhanced if they were occupied by hydrophilic mosses, whose hydration would in turn be enhanced by proximity to water-shedding lichens (Bowker and others 2010). Thus, micro-scale source-sink relationships could mimic those of larger spatial scales where hydrophobic interspaces may shed water to plant-engineered water sinks.

Our study demonstrates that infiltration dynamics in semi-arid Mediterranean ecosystems are best understood and studied as a system. The availability of water for interception by *Stipa* is

largely influenced by the water shedding or harvesting ability of the biological soil crust, and the effect of this crust is in turn largely determined by rabbit activity. The primary means by which these ecosystem engineers influence infiltration is by promoting or destroying the connectivity of macropores to the soil surface, presumably an activity of soil microflora and fauna. The components do not act independently and should not be studied independently. A comprehensive examination of the net effects of the key players in infiltration processes in semi-arid landscapes could be a first step toward integrating our understanding of these natural systems.

## ACKNOWLEDGMENTS

This research was funded by the Spanish Ministerio de Ciencia e Innovación (Grant CGL2008-00986-E/BOS). We thank the Instituto Madrileño de Investigación y Desarrollo Rural, Agrario y Alimentario (IMIDRA) for allowing us to work in the Aranjuez Experimental Station (Finca de Sotomayor). FTM acknowledges support from the European Research Council under the European Community's Seventh Framework Programme (FP7/2007-2013)/ERC Grant agreement no. 242658.

## REFERENCES

- Alexander RW, Calvo A. 1990. The influence of lichens on slope processes in some Spanish badlands. In: Thornes JB, Ed. *Vegetation and erosion*. New York: John Wiley. p 385–98.
- Allen TFH, Starr TB. 1982. *Hierarchy: perspectives for ecological complexity*. Chicago, Illinois: University of Chicago Press.
- Bardgett RD, Anderson JM, Behan-Pelletier V, Brussaard L, Coleman DC, Ettema C, Moldenke A, Schimel JP, Wall DH. 2001. The influence of soil biodiversity on hydrological pathways and the transfer of materials between terrestrial and aquatic ecosystems. *Ecosystems* 4:421–9.
- Bhark EW, Small E. 2003. Association between plant canopies and the spatial patterns of infiltration in shrubland and grassland of the Chihuahuan Desert, New Mexico. *Ecosystems* 5:185–96.
- Bochet E, Rubio JL, Poesen J. 1999. Modified topsoil islands within patchy Mediterranean vegetation in SE Spain. *Catena* 38:23–44.
- Bouma J. 1992. Influence of soil macroporosity on environmental quality. In: Sparks DL, Ed. *Advances in agronomy*, Vol. 46. New York: Academic Press. p 1–37.
- Bowker MA, Soliveres S, Maestre FT. 2010. Competition increases with abiotic stress and regulates the diversity of biological soil crusts. *J Ecol* 98:551–60.
- Brotherson JD, Rushforth SR. 1983. Influence of cryptogamic crusts on moisture relationships of soils in Navajo National Monument, Arizona. *Great Basin Nat* 43:73–8.
- Burnham KP, Anderson DR. 2002. *Model selection and multi-model inference. A practical information-theoretical approach*. Berlin, Germany: Springer-Verlag.

- Cantón Y, Domingo F, Solé-Benet A, Puigdefábregas J. 2002. Influence of soil-surface types on the overall runoff of the Tabernas badlands (south-east Spain): field data and model approaches. *Hydrol Process* 16:2621–43.
- Cantón Y, Solé-Benet A, Domingo F. 2004. Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. *J Hydrol* 285:199–214.
- Casmereiro MA, Molina JA, De la Cruz Caravaca MT, Hernando Costa J, Hernando Massanet MI, Moreno PS. 2003. Influence of scrubs on runoff and sediment loss in soils of Mediterranean climate. *Catena* 57:91–107.
- Cerdá A. 1997. The effect of patchy distribution of *Stipa tenacissima* L. on runoff and erosion. *J Arid Environ* 36:37–51.
- Cook FJ, Broeren A. 1994. Six methods for determining sorptivity and hydraulic conductivity with disc permeameters. *Soil Sci* 157:2–11.
- Darby BJ, Neher DA, Belnap J. 2007. Soil nematode communities are ecologically more mature beneath late-than early-successional stage biological soil crusts. *Appl Soil Ecol* 35:203–12.
- Dean WRJ, Milton SJ. 1991. Patch disturbances in arid grassy dunes: antelope, rodents and annual plants. *J Arid Environ* 20:231–7.
- Dunkerley DL. 2000. Hydrological effects of dryland shrubs: defining the spatial extent of modified soil water uptake rates at an Australian desert site. *J Arid Environ* 45:159–72.
- Eldridge DJ, Freudenberger D. 2005. Ecosystem wicks: woodland trees enhance water infiltration in a fragmented agricultural landscape in eastern Australia. *Austral Ecol* 30:336–47.
- Eldridge DJ, Rosentreter RR. 2004. Shrub mounds enhance water flow in a shrub-steppe community in southwestern Idaho, USA. In: Hild AL, Shaw NL, Meyer S, Booth DT, McArthur ED, Eds. Seed and soil dynamics in shrubland ecosystems. Ogden, Utah: USDA Forest Service RMRS-P-31. pp 77–83.
- Eldridge DJ, Rosentreter RR. 1999. Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. *J Arid Environ* 41:11–25.
- Eldridge DJ, Zaady E, Shachak M. 2000. Infiltration through three contrasting biological soil crusts in patterned landscapes in the Negev, Israel. *Catena* 40:323–36.
- Eldridge DJ, Zaady E, Shachak M. 2002. The impact of disturbance on runoff and sediment production and its implications for the management of desert ecosystems. *Landscape Ecol* 17:587–97.
- Grace JB. 2006. Structural equation modeling and natural systems. Cambridge, UK: Cambridge University Press.
- Herschel JR. 1998. Dune spiders of the Negev desert with notes on *Cerbalus psammodes* (Heteropodidae). *Israel J Zool* 44:243–57.
- James AI, Eldridge DJ, Hill BM. 2009. Foraging animals create fertile patches in an Australian desert shrubland. *Ecography* 32:723–32.
- Jégou D, Schrader S, Diestel H, Cluzeau D. 2001. Morphological, physical and biochemical characteristics of burrow walls formed by earthworms. *Appl Soil Ecol* 17:165–74.
- Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–86.
- Kerley GIH, Whitford WG, Kay FR. 2004. Effects of pocket gophers on desert soils and vegetation. *J Arid Environ* 58:155–66.
- Kidron GJ, Yair A. 1997. Rainfall-runoff relationship over encrusted dune surfaces, Nizzana, western Negev, Israel. *Earth Surf Proc Land* 22:1169–84.
- Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson P, Heal OW, Dhillon S. 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. *Eur J Soil Biol* 33:159–93.
- Loope WL, Gifford GF. 1972. Influence of a soil microfloral crust on select properties of soils under piñon-juniper in south-eastern Utah. *J Soil Water Conserv* 7:128–32.
- López-Portillo J, Montaña C. 1999. Spatial distribution of *Prosopis glandulosa* var. *torreyana* in vegetated stripes of the southern Chihuahuan Desert. *Acta Oecol* 20:197–208.
- Maestre FT, Bautista S, Cortina J, Bellot J. 2001. Potential of using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecol Appl* 11:1641–55.
- Maestre FT, Cortina J. 2002. Spatial patterns of surface soil properties and vegetation in a Mediterranean semi-arid steppe. *Plant Soil* 241:279–91.
- Maestre FT, Cortina J. 2003. Small-scale spatial variation in soil CO<sub>2</sub> efflux in a Mediterranean semiarid steppe. *Appl Soil Ecol* 23:199–209.
- Maestre FT, Huesca M, Zaady E, Bautista S, Cortina J. 2002. Infiltration, penetration resistance and microphytic crust composition in contrasting microsites within a Mediterranean semi-arid steppe. *Soil Biol Biochem* 34:895–8.
- Mitchell PB. 1988. The influences of vegetation, animals and micro-organisms on soil processes. In: Viles HA, Ed. Biogeomorphology. Oxford: Basil Blackwell. p 43–82.
- McCune B, Mefford MJ. 2004. PC-Ord version 5-multivariate analysis of ecological data. Glenden Beach, Oregon, USA: MjM Software.
- Myers KI, Parer I, Wood D, Cooke BD. 1994. The rabbit in Australia. In: Thompson HV, King CM, Eds. The European rabbit: the history and biology of a successful coloniser. New York: Oxford University Press. p 108–57.
- Neher DA, Lewins SA, Weicht TR, Darby BJ. 2009. Microarthropod communities associated with biological soil crusts in the Colorado Plateau and Chihuahuan deserts. *J Arid Environ* 73:672–7.
- Nicolau JM, Solé-Benet A, Puigdefábregas J, Gutiérrez L. 1996. Effects of soil and vegetation on runoff along a catena in semi-arid Spain. *Geomorphology* 14:297–309.
- Parsons AJ, Wainwright J, Schlesinger WH, Abrahams AD. 2003. The role of overland flow in sediment and nitrogen budgets of mesquite dunefields, southern New Mexico. *J Arid Environ* 53:61–71.
- Perroux KM, White I. 1988. Design of disc permeameters. *Soil Sci Soc Am J* 52:1205–13.
- Pugnaire FI, Haase P, Incoll L, Clark SC. 1996. Response of tussock grass *Stipa tenacissima* to watering in a semi-arid environment. *Funct Ecol* 10:265–74.
- Puigdefábregas J, Solé-Benet A, Gutiérrez L, Del Barrio G, Boer M. 1999. Scales and processes of water and sediment redistribution in drylands: results from the Rambla Honda field site in Southeast Spain. *Earth-Sci Rev* 48:39–70.
- Puigdefábregas J, Sanchez G. 1996. Geomorphological implications of vegetation patchiness on semi-arid slopes. In: Anderson MG, Brooks SM, Eds. Advances in hillslope processes, Vol. 2. Chichester, UK: Wiley. p 1027–60.
- Shepherd UL, Brantley SL, Tarleton CA. 2002. Species richness and abundance patterns of microarthropods on cryptobiotic

- crusts in a piñon-juniper habitat: a call for greater knowledge. *J Arid Environ* 52:349–60.
- Scholte TS. 1989. Vegetation–soil relations in an area with sealed Chromic Luvisols, Kenya. *Arid Soil Res Rehabil* 3:337–48.
- Soil Survey Staff. 1994. Keys to soil taxonomy. 6th edn. Washington DC: Soil Conservation Service, USDA.
- Verdú JR, Numa C, Lobo JM, Martínez-Azorín M, Calante E. 2009. Interactions between rabbits and dung beetles influence the establishment of *Erodium praecox*. *J Arid Environ* 73: 713–18.
- Warren SD, Eldridge DJ. 2001. Biological soil crusts and livestock in arid regions: are they compatible? In: Belnap J, Lange O, Eds. *Biological soil crusts: structure, management and function*. Ecological Studies 150. Berlin: Springer-Verlag. p 401–16.
- Wesche K, Nadrowski K, Retzer V. 2007. Habitat engineering under dry conditions: the impact of pikas (*Ochotona pallasi*) on vegetation and site conditions in southern Mongolian steppes. *J Veg Sci* 18:665–74.
- White I. 1988. Tillage practices and soil hydraulic properties: why quantify the obvious? In: Loveday J, Ed. *National soil conference review papers*. Canberra, ACT: Australian Society of Soil Science Incorporated. pp 87–126.
- Whitford WG. 1996. The importance of the biodiversity of soil biota in arid ecosystems. *Biodivers Conserv* 5:185–95.
- Whitford WG, Kay FR. 1999. Biopedurbation by mammals in deserts: a review. *J Arid Environ* 41:203–30.
- Wilkinson MT, Richards PJ, Humphreys GS. 2009. Breaking ground: pedological, geological, and ecological implications of soil bioturbation. *Earth-Sci Rev* 97:257–72.
- Wilson GV, Luxmore RJ. 1988. Infiltration, macroporosity and mesoporosity distributions on two forested watersheds. *Soil Sci Soc Am J* 52:329–35.
- Zaady E, Bouskela A. 2002. Lizard burrows association with successional stages of biological soil crusts in an arid study region. *J Arid Environ* 50:235–46.