Disturbances of Biological Soil Crust by fossorial birds increase plant diversity in a Peruvian desert

María Cristina Rengifo[1,3], Cesar Arana[1,2]

[1]Departamento de Ecología, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, 15072, Perú.
[2]Laboratorio de Ecología y Biogeografía Terrestre de la Facultad de Ciencias Biológicas de la UNMSM, Lima, 15081, Perú.
[3]School of Forestry, Northern Arizona University, 200 E. Pine Knoll Drive, Flagstaff, AZ 86011, USA.

Correspondence to: Maria C. Rengifo (mcr335@nau.edu)

Abstract. The Lomas Formation are fog-dependent oases within the hyper arid band of the Peruvian coast. Biological soil crusts (BSC) form in the Lomas and interact with their fauna and flora. Here we asked if natural disturbances – biopedturbations - made by fossorial birds have an effect on seedling emergence in the Lomas Formations in the National Reserve of Lachay in Lima, Peru. We analysed active and inactive avian biopedturbations, undisturbed BSC and scalped soil field samples for moisture content, soil chemical properties and the seedbank and the field emergence of seedlings. Active biopedturbations had the highest soil moisture content and BSC showed the lowest values. Organic matter content was significantly higher in the BSC than the soil beneath it and the bare soil. However, $CaCO_3$ content and EC were higher in bare soil than the other treatments, and no significant differences were found in soil pH, phosphorus or potassium content between treatments. In the seedbank experiment, 13 herbaceous plant species were found; furthermore, biopedturbations had a higher diversity but lower abundance than the BSC. However, in the field observations biopedturbations had a higher diversity and abundance of seedlings than BSC and only 8 herbaceous species were found. The species *Fuertesimalva peruviana* (L.) Fryxell, *Exodeconus prostratus* (L'Hér.) Raf., *Cryptantha granulosa* I.M. Johnst. *Solanum phyllanthum* Cav. and *Calandrinia alba* (Ruiz & Pav.) D.C increased their abundance in biopedturbations. Our results showed the positive effects on seed germination and diversity of vascular plants by the natural disturbances made by fossorial birds in a unique ecosystem of the Peruvian desert, and demonstrates the importance of spatial and temporal heterogeneity for ecosystem structure and functioning.

1 Introduction

Natural disturbances and their impact in ecological processes has been broadly studied in drylands, and focused extensively on small mammals (Eldridge et al., 2012; Hobbs and Huenneke, 1992; Kerley et al., 2004; Schooley et al., 2000; Whitford and Kay, 1999). Soil disturbances made by burrowing animals directly modify habitats and modulate the availability of resources; by which they are consider ecosystem engineers (Guo, 1996; Hansell, 1993; Jones et al., 1994; Wright et al., 2004). Although it's known that burrowing mammals contribute to the heterogeneity that support different plant communities at small and large scales in landscapes (Eldridge et al., 2012; Whitford and Kay, 1999), very little is described on fossorials birds with similar behavior on drylands.

In the hyperarid system of the Sechura-Atacama Desert, there is a fog oasis known as *Lomas* (Fig 1; Rundel et al., 1991b). Despite the extreme climatic conditions, the coastal hills in *Lomas* are high in biodiversity and endemism of plants and animals (Dillon and Rundel, 1990; Ferreyra, 1983; Pulido et al., 2007). The dry conditions limit the establishment of perennial plants and allow the development of annual vegetation only in the winter months when marine fog and fine drizzle provide water (Ferreyra, 1953). Common birds found in the central Peruvian *Lomas* generate soil disturbances –biopedturbations-. Miners *Geositta* spp. and the burrowing owl *Athene cunicularia* excavate tunnels and create notable mounds in the landscape. These disturbances occur mostly in the low elevation areas of the coastal hills (between 150 and 400 meter) where vegetation cover is limited and the soil cover is dominated by biological soil crust (i.e., BSC) (Ferreyra, 1953). BSC in the central Peruvian *Lomas* has been recently reported for the first time (Arana et al., 2016). A knowledge gap regarding the basics of biocrust ecology, specifically basic structural and taxonomic characterization, nutrient fluxes and interactions with higher taxa, needs to be filled.

This soil community is known as important components of arid ecosystems (Johansen, 1993; Li, 2012; West, 1990). Biological soil crusts found around the world increase the fertility of soils and affect the physical properties of it by altering water infiltration, runoff, albedo, and temperature (Belnap et al., 2016; Bowker et al., 2010; Prasse and Bornkamm, 2000; Weber et al., 2016; West, 1990; Zaady and Shachak, 1994). As a result of those effects, the emergence and survival of vascular plants can be promoted (Jones et al., 1994, 1997). Although effects on vascular plants are more variable and have negative effects are also found depending on BSC and plant characteristics (Boeken and Shachak, 1994; Bowker, 2007; Li et al., 2010), which develops a greater complex scenario for biocrust and vascular plants interactions.

In order to create a basic understanding of the interactions between the components of the *Lomas* ecosystem, we look into the hyperarid system dominated by biocrust and the plant community response to biopedturbations. We hypothesized that the biopedturbations will create a positive effect on plant diversity and might be linked to some abiotic factors. The soil removal and generation of mounds would increase soil moisture content and nutrient availability and increase seed germination. We created a study to specifically test the effects of fossorial birds' disturbances on soil moisture content, physical characteristics, seedbank germination and the emergence of annual plants. The study provides new information on the complexity and functioning of this understudied ecosystem and quantifies the relevance of interaction among its components.

In our study we targeted biopedturbations generated by fossorial birds that are the major disturbing agent in our site. The landscape seen in the lowest part of the hills (*Lomas*) has a flat topography with a narrow inclination that gets steeper going east as we get closer to the top of the hills. The vast area is fully covered with biological soil crust, and only during 4 to 5 months of the wet season we see the establishment of the annual vascular plants. The rest of the year the area lacks higher plants cover. The birds' biopedturbations create bare patches observed with the naked eye across the landscape (Fig. 2). When burrows were active, we targeted the disturbed mounds of soil that have a larger area than the burrow entrance. The soil profile of the mounds has 3 basic layers: an underlying sandy soil, a biocrust layer and another soil layer on top from the burrowing activities of the birds. When burrows are abandoned, the lack of bird activity allows the biocrust organisms in the area to colonize the disturbed top soil, and a new layer is added to the soil profile; and we consider this as the inactive biopedturbations.

2 Methods

2.1 Study site and biopedturbations

The Atacama Desert is a coastal desert that extends 3500 km, from the region north of Trujillo near the Ecuadorian border of Peru, to central Chile (Rundel, 1978). This desert owes its aridity to the persistent temperature inversion associated with the cool north flowing Humboldt Current and the generally stable position of the strong Pacific anticyclone. The Andes Mountains prevent moisture from the east (Houston and Hartley, 2003). The National Reserve of Lachay is located 105 km north from the city of Lima, in the central coast of Peru (S11°23.6', W77°23'). The reserve contains a unique fog and mist-fed ecosystem called Lomas Formations within the hyper arid band of the Peruvian coast (Fig. 1). The landscape is characterized by small hills that create a smooth gradient from 150 m to 750 m of altitude, a mean annual precipitation in the open of 168 mm yr^{-1}. and in the high humidity season, from July until September, a dense fog comes from the sea adds moisture to the hills allowing the establishment of endemic flora (Rundel et al., 1991a).

The study area is located in the lower part of the hills (S11° 23.87', W77° 23.13') in approximately 1.4 km^2 with a smooth gradient from 150 to 250 m of altitude with a mostly flat topography (Fig. 2A). The seasonal vegetation found in the humid season is characterized by the presence of herbaceous plants of rapid flowering. The sandy loam soil is covered by a dark biological soil crust dominated by cyanobacteria (Arana et al., 2016), which is a type of BSC commonly found in warm deserts (Belnap et al., 2001; Pietrasiak, 2014). The BSC is 1-5 mm thick (Fig. 2E), and also has a low percentage (~25%) of moss (*Bryum argenteum* Hedw mostly) and some crustose and fruticose lichens. In this landscape three species of fossorial birds are the main agents of biopedturbations: the burrowing owl (*Athene cunicularia*), the coastal miner (*Geositta peruviana*) and the greyish miner (*Geositta maritima*).

For the purpose of this study we targeted the mound of removed soil that is placed over the surface as the biopedturbation (Fig. 2A-C). The birds break the BSC to create their burrows and the removed soil is placed on top of biocrust. We aimed for the average mounds that had an area of approximately 0.6 m^2; mostly from miners and some small ones from the burrowing owls. In the study area mounds of the two species of miners are indistinguishable one from another and range from 0.08 to 0.7 m^2. The mounds of the burrow owl are usually bigger and range between 0.4 to 1.3 m^2 (Unpublished data). We targeted active and inactive biopedturbations, the active ones were considered from the active burrows where the activity of the birds keep the top soil of the mound loose. Inactive biopedturbations were the mounds that were colonized by an early successional biocrust as a result of an abandoned burrow.

2.2 Moisture content

We examined the top 5 cm of soil moisture content between active and inactive biopedturbations, biological soil crust and scalped soil (Fig. 3). We established 26 experimental sites, 15 for active biopedturbations and 11 for inactive biopedturbations. Each experimental site consisted of three 30 x 30 cm plots placed not more than 1 m of separation: a scalped soil plot, a biopedturbation plot, and a BSC plot. The scalped soil plot was an 30x30 cm area where the surface layer of BSC was removed to simulate bare soil surface. The biopedturbation plot was an area marked on the mound of sand, and the BSC plot was an area with undisturbed BSC. Selected biopedturbations were separated at least 10 m.

After two months of the BSC removal in the scalped soil plot, we sampled 100 g of the top 5 cm of soil inside each plot. Samples were collected in hermetic bags, and later in the laboratory were weighted, dried in an oven for 24 h at 105 °C, reweighed and their gravimetric moisture content calculated (Yair et al., 2011). Each sample represented a small fraction of the 0.09 m^2 area. The sampling collection was made at the end of October of 2015. This was an anomalous year influenced by the ENSO, 0 mm of precipitation was register in October, when 0.2 mm was expected.

$$Water\ content\ (\%) = \frac{w_w - w_d}{w_d} x\ 100$$

Where W_w is the weight of wet soil in grams and W_d is the weight of dry soil.

2.3 Soil chemical properties

To examine the soil chemical properties of the different layers of a biopedturbations we considered three soil treatments: (1) The undisturbed layer of BSC, (2) the underlying soil of 5 cm deep which was directly below the initially undisturbed layer of BSC sampled, and (3) the biopedturbation soil from the loose sand of the mound. Each treatment was replicated three times. The biopedturbations were separated by at least 10 m, and we used the undisturbed BSC next to each biopedturbation to diminish environmental heterogeneity. Every soil sample weighted approximately 500 g. The routine soil analysis included the available phosphorus (P), exchangeable potassium (K), calcium carbonate ($CaCO_3$), soil organic matter (O.M.), pH and electrical conductivity (E.C.), and was made by the Water, Soil and Environment Analysis Laboratory (LAASMA) of the Universidad Nacional Agraria La Molina, in Lima.

2.4 Seedbank evaluation

To evaluate the seed bank between biopedturbations and the soil covered with BSC, we took paired samples of soil from the mounds and from the undisturbed BSC next to the mound. Each soil sample was taken from a 10x10 cm area and 5cm deep; the paired samples were separated by approximately 1 m. We used 27 active biopedturbations and 34 inactive biopedturbations, each paired with an undisturbed BSC sample.

We conducted the experiment in a greenhouse at the UNMSM. The bagged soil samples were placed in plastic trays and arranged in a Latin Square design to eliminate positional effects within the greenhouse. The trays were watered regularly every two days with tap water, and the number of seedlings were recorded at frequent intervals. The germination beyond five weeks was found negligible and during the germination period there was no soil disturbances and seedling were removed only at the end of the experiment. The taxonomic determinations of species were made with dichotomous keys and specialized bibliography (Fryxell, 1996; Krapovickas, 2007; Lleellish et al., 2015; Sagástegui and Leiva, 1993; Tate, 2011).

2.5 Field seedlings emergence

We established a new set of plots in the field to observe the natural seedling emergence. We marked 30 x 30 cm paired plots, one on the biopedturbation and the other one in the undisturbed BSC, separated 1 m from each other. Paired sampling was need to diminish the environmental heterogeneity and compare plots with similar conditions due their proximity. We consider 15 replicates for active biopedturbations and 15 for inactive ones. In every plot we count and identify all the present seedlings. We evaluated the seedlings emergence at the beginning of the wet season in August 2016.

2.6 Statistical analysis

To determine if mounds, bare soil or BSC had different soil moisture, we used nonparametric related-samples Wilcoxon signed-rank test, to compare the median of paired samples. Soil chemical properties were compared in pairs with the nonparametric Independent-sample median test. Plant diversity was calculated with Fisher's alpha index defined by the formula $S=a*\ln(1+n/a)$ where S is number of taxa, n is number of individuals and a is the Fisher's alpha. We used PAST Paleontological Statistic software version 3.0 to extract the diversity index. Plant abundance values didn't go through any transformation. Plant diversity index and abundance values were analyzed by pairs using nonparametric related samples Wilcoxon signed-rank test. All the statistical nonparametric analyses were made in Software SPSS version 19, and $\alpha=0.05$ for every case. Plant density was calculated by the sum of all seedling divide by number of samples and the area sampled in m^2.

3 Results

3.1 Soil moisture content

Soil moisture content showed different patterns among active and inactive biopedturbations. Active biopedturbations have the highest moisture content (0.71% ±0.164) among the soil treatments (Wilcoxon signed-rank test, $p=0.041$ paired to scalped soil, $p=0.002$ paired to BSC). On the other hand, inactive biopedturbations (0.66% ± 0.164) have similar moisture content than scalped soil (0.71% ± 0.152) and that BSC (0.58% ± 0.152). Biological soil crust showed to have the lowest moisture content in both types of biopedturbations (Wilcoxon signed-rank test, $p<0.05$ for active and inactive biopedturbations).

3.2 Chemical properties

Our results show that no significant difference in the potassium and phosphorous content among the BSC layer, the underlying soil or the biopedturbation soil (Independent-sample median test, $p>0.05$). The percentage of soil organic matter in the BSC layer (0.67%) was significantly higher than the underlying soil (0.38%) and the biopedturbation soil (0.27%), Independent-sample test $p=0.043$; and no difference was found between the organic matter values of the underlying soil and the biopedturbation soil. The pH values remained similar among the treatments. Calcium carbonate and electric conductivity values showed the same trend between treatments, where the highest values were found in the biopedturbation soil, and the BSC layer and the underlying soil had similar values (Table 1).

3.3 Effects on plant germination

We found 13 different native plant species germinated from the overall seedbank. Among treatments, active biopedturbations had a mean of 10.5 germinated seeds, significantly lower (Wilcoxon signed rank test, $p=0.001$) than the27.4 germinated seeds in the paired BSC. Inactive biopedturbations had the same trend, with a mean of 21.2 germinated seeds, significantly lower (Wilcoxon signed-rank test, $p=0.046$) than the 33.1 germinated seeds of the paired BSC. (Fig 3). The Fisher's alpha diversity index of germinated species was 1.05, and significantly higher than the 0.76 of the paired BSC (Wilcoxon signed-rank test, $p=0.035$), but the same trend was not statistically supported for diversity in active biopedturbations. The number of species expected in the rarefaction curves was similar between treatments. Nevertheless, the BSC had a lower expected richness compared to their paired active biopedturbations (Fig. 5)

In field observations (Table 2) we recorded the emergence of only eight species at the beginning of the wet season. In contrast to the abundance found in the seedbank, the natural seedling emergence was higher in biopedturbations, active biopedturbations had a mean of 21.9 seedlings, significantly higher than the mean 11 seedlings in the paired BSC (Wilcoxon signed-rank test, $p=0.011$). Inactive biopedturbations showed the same trend, with a mean of 12.5 seedlings, significantly higher than the 8.2 seedling in BSC (Wilcoxon signed-rank test, $p=0.020$). The diversity of seedlings between treatments was not significantly different, although inactive biopedturbations had a slightly higher diversity index compared to the paired BSC (Wilcoxon test, p=0.507). The number of expected species in the rarefaction curves are higher in both active and inactive biopedturbations compared to their paired BSC. Inactive biopedturbations shows the highest expected richness between treatments (Fig. 5)

The floristic composition (Table 2) shows that *Cistanthe paniculata* is the species with the highest density in every treatment, except for the inactive biopedturbations in the field observations, where the species with the highest density is *Fuertesimalva peruviana*. We found species that have a higher density in inactive biopedtubations in both the seedbank and in the natural emergence: *Exodeconus prostratus, Solanum phyllanthum* and *Calandrinia alba*. An additional species, *Cryptantha limensis* also show a higher abundance in inactive biopedturbations in the field observations but without the same pattern in the seedbank.

4 Discussion

Our study is the first to look at how biopedturbation by fossorial birds alters the soil chemistry, moisture and potential for plant germination in the Lomas region of the Atacama Desert. This area is fully covered in dark cyanobacterial biocrusts except where burrowing activity has occurred. Burrowing fossorial birds are acting as ecosystem engineers, opening up niches for plant germination. Our work shows that biopedturbations had a positive effect on the plant community by increasing the germinating plant diversity in the transition to wet season. Some annual plant species benefit from both active and inactive biopedturbations.

Effects of biopedturbation on soil moisture

Areas with BSC presented the lowest values of soil moisture content, that is a possible result of a low water infiltration, because the BSC tends to seal the soil surface (Brotherson and Ruthforth, 1983; Zhang et al., 2010). Factors like biological soil crust characteristics, the topography and soil types (Chamizo et al., 2012) can cause BSC to increase (Brotherson and Ruthforth, 1983; Bu et al., 2015) or decrease (Eldridge et al., 2000; Gao et al., 2010; Kidron and Yair, 1997; Yair, 1990) infiltration rates in the soil. It was suggested that in sandy soils the BSC decrease the infiltration as a result from the reduction in the porosity (Warren, 2001). The biological soil crust of our study may decreased the water infiltration and as a consequence diminish the soil moisture content, this results also agreed with studies in the Negev desert (Eldridge et al., 2000; Keck et al., 2016) which resembles physical characteristics of our studied area. Whereas the cyanobacteria and lichens of the BSC decrease the permeability of the soil (Loope and Gifford, 1972), the bare soil doesn’t (Keck et al., 2016). Our data shows the same results, where the scalped soil had higher moisture content than BSC, that could be explained by the permeability, because biological soil crust tend to seal the soil surface (Booth, 1941; Brotherson and Ruthforth, 1983; George et al., 2003) and consume the water available in the most superficial soil layer (Bu et al., 2015; Gao et al., 2010)

On the other hand, biopedturbations present higher values of moisture content. In the case of active biopedturbations, moisture content was higher than the other soil surfaces, but the inactive biopedturbations show similar moisture content than the bare soil. We hypothesized that the soil profile of active biopedturbation (Fig. 3) allows water to infiltrate easily through the first layer of sand, and because of the hydrophobic characteristics and the water absorption of biocrust organisms (Kidron et al., 1999; Rodríguez-Caballero et al., 2013) in the buried BSC layer the moisture is better retained, compared to the bare soil and the soil cover with BSC. Our results differed completely with a study in Northern Negev of Israel (Boeken and Shachak, 1994) that found that man-made mounds consistently presented the lowest moisture content compare to the BSC matrix, the main difference with this study is the characteristic of the man-made mounds, that were bigger and taller than the bird mounds. The soil moisture content on the first 15 cm was only loose soil, where in our study the first 5cm involves the BSC layer. The inactive biopedturbation, has an additional incipient BSC layer that could diminish the water infiltration by reduction of porosity and the consumption of the water available in the most superficial soil layer and the (Bu et al., 2015; Gao et al., 2010; Warren, 2001), but not as much as a well develop BSC that shows the lowest values among treatments. As a result, the moisture content in inactive biopedturbations is similar to the scalped soil and to the BSC.

Effects of biopedturbation on soil chemistry

The soil chemical properties give us an approximation on the disturbance effect of the fossorial birds. Although many physical and chemical soil characteristics are insightful way to understand the ecological and biochemical processes occurring in the system, our study resources limited the extent of measurable characteristics. A basic routine soil analysis provided an insight of soil fertility and compared if the biopedturbations generate a great effect on those characteristics.

The nutrients potassium and phosphorus and the pH didn't show statistical differences between treatments, suggesting that the bird's biopedturbations do not alter significantly the nutrient soil content. Potassium values were slightly higher in the BSC, which is expected since it has been established before that BSC increases the soil fertility (Belnap and Harper, 1995; Harper and Pendleton, 1993). Though also bird droppings may contribute to soil fertility, our results did not support it. Differences in carbon or nitrogen content might be a better indicator of fertility, and thorough studies should be done in the *Lomas* environment. Soil pH has been reported in other studies to not be significantly altered by the presence of BSC (Evans and Johansen, 1999; Guo et al., 2008; Kidron et al., 2015), and our results suggest the same. Soil organic matter was expected to be higher in the BSC in comparison with the underlying and biopedturbation soil, since is directly related to the organic carbon and BSC have high concentration of organism living in it (Delgado-Baquerizo et al., 2016; Guo et al., 2008). organic matter content, suggesting that neither the occasional bird droppings, nor the destruction and removal of the BSC increases the organic matter in the other soil surfaces.

Unlike other studies (Guo et al., 2008), calcium carbonate content was not higher in the BSC, instead the biopedturbation soil had the higher values, this results may be explained by the abundant remains of gastropods shell's present in the locality, and not a reflection of increase nutrients in the soil. At the same time, since electric conductivity is influenced by the concentration of calcium carbonate BSC did not show high values of EC; despite being expected due to the concentration of ions released by the decomposition of microorganisms. Although some differences in chemical properties where found and were expected, the lack of significant variation in K and P nutrients and pH between treatments shows that the biopedturbations might not have a greater effect on those soil characteristics due to the small area affected and may not have a great contribution in plant establishment.

Biopedturbation effects on plant communities

The plant community responded different in the greenhouse experiments than in the field emergence observations. Studies on BSC effects on vascular plants germination and establishment have contradictory results (Bowker, 2007) some consider that BSC can affect negatively plant density (Johansen, 1993; Prasse and Bornkamm, 2000), other showed the positive effect in semiarid ecosystems (Boeken et al., 2004; Defalco et al., 2001) and many species-specific effects (Hawkes, 2004; Su et al., 2009). By stop the limitation of water availability on the soil, the total germination of the seed bank in the greenhouse represent the total viable seeds contained in the first 5cm of the soil (Thompson and Grime, 1979; Zhang et al., 2010). We found that biopedturbations are significantly less abundant in seeds of annual vascular plants in contrast with the BSC; nevertheless, are more diverse and rich in species composition. Even though a smooth biocrust increases the chances that seed may be taken by the wind (Belnap, 2006; Boeken and Shachak, 1994), plant litter annually accumulated on the soil surface remain along with a large seed load. The mounds of sand over the BSC do not present the same quantity of plant litter and as a consequence it would be expected to have less seeds. A higher diversity in biopedturbations suggests a positive effect in the vegetation composition, but it would be necessary to study more thoroughly this phenomenon to understand if those biopedturbations work as a seed trap, if the higher diversity is product of the soil removal, or if the loose soil creates a better new topography compared to the tightly woven BSC surface (Boeken and Shachak, 1994).

Our field data taken in the transition from dry season to wet season shows that biopedturbations have higher abundance and diversity in contrast with the BSC. Since the seedbank is more abundant in the BSC, the low emergence in the field compared to biopedturbations might be explained by the soil moisture content, that we found to be higher in the biopedturbations. And, although diversity was no significantly different, biopedturbations in the field show a higher species richness as seen in the seed bank.
Moreover, biopedturbations had a positive effect in some specific species: *Fuertesimalva peruviana*, in spite of been a high density specie in the BSC, almost quadrupled its abundance in active and inactive biopedturbations in the field, and doubled

its seedbank density. *Exodeconus prostratus* the species with the lowest density in the field was only found in inactive biopedturbations and contained a greater seedbank in both active and inactive biopedturbations. *Cryptantha limensis* besides having a greater seedbank in BSC it showed a higher plant density in the biopedturbations. *Solanum phyllantum* and *Calandrinia alba* had a greater seed bank density in inactive biopedturbations and consequently showed a higher density when emerge from inactive biopedturbations (Table 2). We hypothesized that some plant species benefit from the higher moisture content in the active biopedturbations, and some may also be favored by other characteristics of the biopedturbations. Nevertheless, we show the positive species-specific effect of biopedturbation on plant, which contributes to the plant community composition of the area.

Fossorial birds as ecosystem engineers: interactions and impacts on plant communities

The three components of the ecosystem studied have a series of interactions, thus we cannot cover them all we took a glance to the complex system. Fossorial birds destroy a small portion of BSC to create their burrows, and at the same time create an area where biological soil crust is buried under a mound of sand, which we called biopedturbations. This burial causes a negative effect on the biocrust organisms by stressing them (Rao et al., 2012). The full net of interaction between biological soil crust and vegetation is highly complex and we cannot explain it completely. We based many of our assumptions on literature to reduce the complexity. We understand that BSC can have a positive effect (Belnap and Büdel, 2016; Boeken, 2008; Hawkes, 2004) and at the same time a negative effect on seed germination and establishment (Booth, 1941; Brotherson and Ruthforth, 1983; George et al., 2003; Johansen, 1993; Prasse and Bornkamm, 2000; Zhang et al., 2016, 2010). At the same time, vegetation could also provide a positive effect to the BSC in our system, by increasing soil organic matter and soil fertility (Bowker, 2007; Li et al., 2007; Maestre et al., 2010). At last, the biopedturbations made by fossorial birds create small patches in the landscape where soil moisture was enhanced, soil nutrients were not altered and a disturbed surface was present, in contrast with the BSC matrix, in which resulted in more seedling germination and higher plant diversity in the transition from dry to wet season.

Fossorial birds cause biopedturbations that affect ecosystem functions, and can therefore be considered ecosystem engineers (Jones et al., 1994). This is consistent with the intermediate disturbance hypothesis (Connell, 1978), where moderate disturbances maximize the species diversity in the system, and increase the special and temporal heterogeneity important for the maintenance of ecosystem biodiversity, structure and functioning (Huston, 1994; Pickett and White, 1985)

Data availability. The data is available in the supplement of this article.

Author contribution. MR and CA designed the research. MR collected samples from the field and did all the measurements. MR and CA analyzed the data. MR prepared the manuscript with corrections from CA.

Competing interests. The authors declare that they have no conflict of interest.

Special issue statement. This article is part of the special issue “Biological soil crust and their role in biogeochemical processes and the cycling”. It is not associated with a conference.

Acknowledges. We are grateful to Mery Suni, Tomás A. Carlo and friends of the Ecology Department of the Natural History Museum for the invaluable help and support in the development of this work. We also thank the Natural History Museum of Lima and the heads of the National Reserve of Lachay for the institutional support. Our gratitude extends to Anita Antoninka for her valuable help and support through the manuscript corrections. Furthermore, the present work was part of the undergraduate thesis of Maria C. Rengifo, and was possible thanks to the financial support of the Universidad Nacional

Mayor de San Marcos through the Vicerectorado de Investigación and the Instituto de Ciencias Biológicas Antonio Raimondi.

References

Arana, C., Carlo, T. A. and Salinas, L.: Biological soil crust in Peru: first record and description, Zo. Áridas, 16(1), 112, doi:10.21704/za.v16i1.632, 2016.

Belnap, J.: The potential roles of biological soil crusts in dryland hydrologic cycles, Hydrol. Process., 20(15), 3159–3178, doi:10.1002/hyp.6325, 2006.

Belnap, J. and Büdel, B.: Biological Soil Crusts as Soil Stabilizers, in Biological Soil Crusts: An Organizing Principle in Drylands, pp. 305–320., 2016.

Belnap, J. and Harper, K. T.: Influence of Cryptobiotic Soil Crusts on Elemental Content of Tissue of Two Desert Seed Plants, Arid Soil Res. Rehabil., 9(2), 107–115, doi:10.1080/15324989509385879, 1995.

Belnap, J., Rosentreter, R., Leonard, S., Kaltenecker, J. H., Williams, J. and Eldridge, D. J.: BIOLOGICAL SOIL CRUSTS : Technical Reference 1730-2, Management, 2001.

Belnap, J., Weber, B. and Büdel, B.: Biological Soil Crusts as an Organizing Principle in Drylands, in Biological Soil Crusts: An Organizing Principle in Drylands, pp. 3–13., 2016.

Boeken, B.: The role of seedlings in the dynamics of dryland ecosystems – their response to and involvement in dryland heterogeneity, degradation, and restoration, [online] Available from: http://www.bgu.ac.il/desert_agriculture/Vegecology/Papers/Boeken2008.pdf (Accessed 17 December 2017), 2008.

Boeken, B. and Shachak, M.: Desert Plant Communities in Human-Made Patches--Implications for Management, Source Ecol. Appl., 4(4), 702–716 [online] Available from: http://www.jstor.org/stable/1942001 (Accessed 17 December 2017), 1994.

Boeken, B., Ariza, C., Gutterman, Y. and Zaady, E.: Environmental factors affecting dispersal , germination and distribution of Stipa capensis in the Negev Desert , Israel, Ecol. Res., 19(April), 533–540, doi:10.1111/j.1440-1703.2004.00666.x, 2004.

Booth, W. E.: Algae as pioneers in plant succession and their importance in erosion control, Ecology, 22(1), 38–46 [online] Available from: http://www.jstor.org/stable/1930007, 1941.

Bowker, M. a.: Biological soil crust rehabilitation in theory and practice: An underexploited opportunity, Restor. Ecol., 15(1), 13–23, doi:10.1111/j.1526-100X.2006.00185.x, 2007.

Bowker, M. A., Maestre, F. T. and Escolar, C.: Biological crusts as a model system for examining the biodiversity-ecosystem function relationship in soils, Soil Biol. Biochem., 42(3), 405–417, doi:10.1016/j.soilbio.2009.10.025, 2010.

Brotherson, J. D. and Ruthforth, S. R.: Influence Of Cryptogamic Crusts on Moisture Relationships of Soils in Navajo National Monument , Arizona, West. North Am. Nat., 43, 73–78, doi:10.2307/41711969, 1983.

Bu, C., Wu, S., Han, F., Yang, Y. and Meng, J.: The Combined Effects of Moss-Dominated Biocrusts and Vegetation on Erosion and Soil Moisture and Implications for Disturbance on the Loess Plateau , China, , 1–15, doi:10.1371/journal.pone.0127394, 2015.

Chamizo, S., Cantón, Y., Lázaro, R., Solé-Benet, A. and Domingo, F.: Crust Composition and Disturbance Drive Infiltration Through Biological Soil Crusts in Semiarid Ecosystems, Ecosystems, 15(1), 148–161, doi:10.1007/s10021-011-9499-6, 2012.

Connell, J. H.: Diversity in Tropical Rain Forests and Coral Reefs High diversity of trees and corals is maintained, Science (80-.)., 199(4335), 1302–1310, 1978.

Defalco, L. A., Detling, J. K., Tracy, C. R. and Warren, S. D.: Physiological variation among native and exotic winter annual plants associated with microbiotic crusts in the Mojave Desert, Plant Soil, 234, 1–14, doi:10.1023/A:1010323001006, 2001.

Delgado-Baquerizo, M., Maestre, F. T., Eldridge, D. J., Bowker, M. A., Ochoa, V., Gozalo, B., Berdugo, M., Val, J. and Singh, B. K.: Biocrust-forming mosses mitigate the negative impacts of increasing aridity on ecosystem multifunctionality in drylands, New Phytol., 209(4), 1540–1552, doi:10.1111/nph.13688, 2016.

Dillon, M. O. and Rundel, P. W.: The Botanical Response of the Atacama and Peruvian Desert Floras to the 1982-83 El Niño Event, in Elsevier Oceanography Series, vol. 52, pp. 487–504., 1990.

Eldridge, D. J., Zaady, E. and Shachak, M.: Infiltration through three contrasting biological soil crusts in patterned landscapes in the Negev, Israel, CATENA, 40(3), 323–336, doi:10.1016/S0341-8162(00)00082-5, 2000.

Eldridge, D. J., Koen, T. B., Killgore, A., Huang, N. and Whitford, W. G.: Animal foraging as a mechanism for sediment movement and soil nutrient development: Evidence from the semi-arid Australian woodlands and the Chihuahuan Desert, Geomorphology, 157–158, 131–141, doi:10.1016/j.geomorph.2011.04.041, 2012.

Evans, R. D. and Johansen, J. R.: Microbiotic crusts and ecosystem processes, CRC. Crit. Rev. Plant Sci., 18(2), 183–225, doi:10.1016/S0735-2689(99)00384-6, 1999.

Ferreyra, R.: Comunidades vegetales de algunas lomas costaneras del Peru., Bol. Est. Exp. Agr. La Molina [online] Available from: http://ci.nii.ac.jp/naid/10006693974/, 1953.

Ferreyra, R.: Los tipos de vegetación de la costa peruana, An. Jard. Bot. Madrid, 40(1), 241–256, 1983.

Fryxell, P. A.: Sida: Contributions to Botany, Sida, 17(1), 69–76, doi:10.2307/1223953, 1996.

Gao, S., Ye, X., Chu, Y. and Dong, M.: Effects of biological soil crusts on profile distribution of soil water, organic carbon and total nitrogen in Mu Us Sandland, China, J. Plant Ecol., 3(4), 279–284, doi:10.1093/jpe/rtq015, 2010.

George, D. B., Roundy, B. A., St. Clair, L. L., Johansen, J. R., Schaalje, G. B. and Webb, B. L.: The Effects of Microbiotic Soil Crustson Soil Water Loss, Arid L. Res. Manag., 17(2), 113–125, doi:10.1080/15324980301588, 2003.

Guo, Q.: Effects of Bannertail Kangaroo Rat Mounds on Small-Scale Plant Community, Oecologia, 106(2), 247–256, 1996.

Guo, Y., Zhao, H., Zuo, X., Drake, S. and Zhao, X.: Biological soil crust development and its topsoil properties in the process of dune stabilization, Inner Mongolia, China, Environ. Geol., 54(3), 653–662, doi:10.1007/s00254-007-1130-y, 2008.

Hansell, M. H.: The Ecological Impact of Animal Nests and Burrows, Funct. Ecol., 7(1), 5, doi:10.2307/2389861, 1993.

Harper, K. T. and Pendleton, R. L.: Cyanobacteria and cyanolichens, can they enhance availability of essential minerals for higher plants?, Gt. Basin Nat., 53(1), 59–72 [online] Available from: http://www.jstor.org/stable/41712758, 1993.

Hawkes, C. V.: Effects of biological soil crusts on seed germination of four endangered herbs in a xeric Florida shrubland during drought, Plant Ecol., 170(1), 121–134, doi:10.1023/B:VEGE.0000019035.56245.91, 2004.

Hobbs, R. J. and Huenneke, L. F.: Disturbance , Diversity , and Invasion : Implications for Conservation, , 6(3), 324–337, 1992.

Huston, M. A.: Biological Diversity The coexistence of species on changing landscapes, Cambridge University Press., 1994.

Johansen, J. R.: Cryptogamic Crust of Semiarid and Arid Lands of North America, J. Phycol., 29(2), 140–147, doi:10.1111/j.0022-3646.1993.00140.x, 1993.

Jones, C. G., Lawton, J. H. and Shachak, M.: Organisms as ecosystem engineers, OIKOS, 69(3), 373–386, 1994.

Jones, C. G., Lawton, J. H. and Shachak, M.: Positive and negative effects of organisms as physical ecosystem engineers, Ecology, 78(7), 1946–1957, doi:10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2, 1997.

Keck, H., Felde, V. J. M. N. L., Drahorad, S. L. and Felix-Henningsen, P.: Biological soil crusts cause subcritical water repellency in a sand dune ecosystem located along a rainfall gradient in the NW Negev desert, Israel, J. Hydrol. Hydromechanics, 64(2), 133–140, doi:10.1515/johh-2016-0001, 2016.

Kerley, G. I. H., Whitford, W. G. and Kay, F. R.: Effects of pocket gophers on desert soils and vegetation, , 58, 155–166, doi:10.1016/j.jaridenv.2003.08.001, 2004.

Kidron, G. J. and Yair, A.: Rainfall–runoff relationship over encrusted dune surfaces, Nizzana, Western Negev, Israel, Earth Surf. Process. Landforms, 22(12), 1169–1184, doi:10.1002/(SICI)1096-9837(199712)22:12<1169::AID-ESP812>3.0.CO;2-C, 1997.

Kidron, G. J., Yaalon, D. H. and Vonshak, A.: Two causes for runoff initiation on microbiotic crusts: Hydrophobicity and pore clogging, Soil Sci., 164, 18–27 [online] Available from: http://ovidsp.tx.ovid.com/sp-3.27.2b/ovidweb.cgi?&S=IAJKFPBEAFDDPMILNCFKFAFBOEKGAA00&Link+Set=S.sh.44%7C1%7Csl_10, 1999.

Kidron, G. J., Posmanik, R., Brunner, T. and Nejidat, A.: Spatial abundance of microbial nitrogen-transforming genes and inorganic nitrogen in biocrusts along a transect of an arid sand dune in the Negev Desert, Soil Biol. Biochem., 83, 150–159, doi:10.1016/j.soilbio.2015.01.024, 2015.

Krapovickas, A.: Notas sobre Urocarpidium y Fuertesimalva (Malvaceae), Bonplandia, 24(1), 43–49, 2007.

Li, J., Zhao, C., Zhu, H., Li, Y. and Wang, F.: Effect of plant species on shrub fertile island at an oasis–desert ecotone in the South Junggar Basin, China, J. Arid Environ., 71(4), 350–361, doi:10.1016/J.JARIDENV.2007.03.015, 2007.

Li, X. R.: Eco-hydrology of biological soil crusts in desert regions of China, China High. Educ. Press, 2012.

Li, Y., Wang, Z., Xu, T., Tu, W., Liu, C., Zhang, Y. and Yang, C.: Reorganization of photosystem II is involved in the rapid photosynthetic recovery of desert moss Syntrichia caninervis upon rehydration, J. Plant Physiol., 167(16), 1390–1397, doi:10.1016/j.jplph.2010.05.028, 2010.

Lleellish, M., Odar, J. and Trinidad, H.: Guía de Flora de las Lomas de Lima, Servicio Nacional Forestal y de Fauna Silvestre, Lima, Peru., 2015.

Loope, W. L. and Gifford, G.: Influence of a soil microfloral crust on select properties of soils under pinyon-juniper in southeastern Utah, J. Soil Water Conserv., 27, 164–167 [online] Available from: http://agris.fao.org/agris-search/search.do?recordID=US201302323378, 1972.

Maestre, F. T., Bowker, M. A., Escolar, C., Puche, M. D., Soliveres, S., Maltez-Mouro, S., García-Palacios, P., Castillo-Monroy, A. P., Martínez, I. and Escudero, A.: Do biotic interactions modulate ecosystem functioning along stress gradients? Insights from semi-arid plant and biological soil crust communities., Philos. Trans. R. Soc. Lond. B. Biol. Sci., 365(1549), 2057–2070, doi:10.1098/rstb.2010.0016, 2010.

Pickett, S. T. A. and White, P. S.: The Ecology of Natural Disturbance and Patch Dynamics, edited by S. Pickett and P. S. White. [online] Available from: http://www.sciencedirect.com/science/book/9780125545204, 1985.

Pietrasiak, N.: Field Guide to Classify Biological Soil Crusts for Ecological Site Evaluation, USDA-NRCS Tech. Ref., in review [online] Available from: https://www.nrcs.usda.gov/wps/PA_NRCSConsumption/download?cid=stelprdb1263524&ext=pdf, 2014.

Prasse, R. and Bornkamm, R.: Effect of Microbiotic Soil Surface Crusts on Emergence of Vascular Plants, Plant Ecol., 150(1), 65–75 [online] Available from: http://www.jstor.org/stable/20050979, 2000.

Pulido, V., Salinas, L. and Arana, C.: Aves en el desierto de ica La Experiencia de Agrokasa., 2007.

Rao, B., Liu, Y., Lan, S., Wu, P., Wang, W. and Li, D.: Effects of sand burial stress on the early developments of cyanobacterial crusts in the, Eur. J. Soil Biol., 48(February), 48–55, doi:10.1016/j.ejsobi.2011.07.009, 2012.

Rodríguez-Caballero, E., Cantón, Y., Chamizo, S., Lázaro, R. and Escudero, A.: Soil Loss and Runoff in Semiarid Ecosystems: A Complex Interaction Between Biological Soil Crusts, Micro-topography, and Hydrological Drivers, Ecosystems, 16(4), 529–546, doi:10.1007/s10021-012-9626-z, 2013.

Rundel, P. W.: Ecological Relationships of Desert Fog Zone Lichens, Am. Bryol. Lichenol. Soc., 81(2), 277–293 [online] Available from: http://www.jstor.org/stable/3242189, 1978.

Rundel, P. W., Dillon, M. O., Palma, B., Mooney, H. a., Gulmon, S. L. and Ehleringer, J. R.: The phytogeography and ecology of the coastal Atacama and Peruvian deserts, Aliso, 13(1), 1–49, 1991a.

Rundel, P. W., Dillon, M. O., Palma, B., Mooney, H. A., Gulmon, S. L. and Ehleringer, J. R.: The Phytogeography and Ecology of the Coastal Atacama and Peruvian Deserts, , 13(1), 1991b.

Sagástegui, A. and Leiva, S.: Flora invasora de los cultivos del Perú Edit, Lib. EIRL Trujillo-Perú, 1993.

Schooley, R. L., Bestelmeyer, B. T. and Kelly, J. F.: Influence of small-scale disturbances by kangaroo rats on Chihuahuan Desert ants, Oecologia, 125(1), 142–149, doi:10.1007/PL00008885, 2000.

Su, Y. G., Li, X. R., Zheng, J. G. and Huang, G.: The effect of biological soil crusts of different successional stages and conditions on the germination of seeds of three desert plants, J. Arid Environ., 73(10), 931–936, doi:10.1016/j.jaridenv.2009.04.010, 2009.

Tate, A.: The status of Urocarpidium (Malvaceae): Insight from nuclear and pastid-based phylogenies, Taxon, 60(5), 1330–1338, 2011.

Thompson, K. and Grime, J. P.: Seasonal Variation in the Seed Banks of Herbaceous Species in Ten Contrasting Habitats, J. Ecol., 67(3), 893, doi:10.2307/2259220, 1979.

Warren, S. D.: Synopsis: Influence of Biological Soil Crusts on Arid Land Hydrology and Soil Stability, in Biological Soil Crusts: Structure, Function, and Management, pp. 349–360., 2001.

Weber, B., Büdel, B. and Belnap, J.: Biological Soil Crusts: An Organizing Principle in Drylands, edited by B. Weber, B. Büdel, and J. Belnap, Springer International Publishing, Cham., 2016.

West, N. E.: Structure and function of soil microphytic crusts in wildland ecosystems of arid and semi-arid regions, Adv. Ecol. Res., 20, 179–223, doi:10.1016/S0065-2504(08)60055-0, 1990.

Whitford, W. G. and Kay, F. R.: Biopedturbation by mammals in deserts: a review, J. Arid Environ., 41(2), 203–230, doi:10.1006/jare.1998.0482, 1999.

Wright, J. P., Gurney, W. S. C. and Jones, C. G.: Patch dynamics in a landscape modified by ecosystem engineers, Oikos, 105(2), 336–348, doi:10.1111/j.0030-1299.2004.12654.x, 2004.

Yair, A.: Runoff Generation I N a Sandy Area-the Sands , Western Negev , Israel, Earth Surf. Process. Landforms, 15, 597–609, 1990.

Yair, A., Almog, R. and Veste, M.: Differential hydrological response of biological topsoil crusts along a rainfall gradient in a sandy arid area: Northern Negev desert, Israel, Catena, 87(3), 326–333, doi:10.1016/j.catena.2011.06.015, 2011.

Zaady, E. and Shachak, M.: Microphytic soil crust and ecosystem leakage in the Negev Desert, Am. J. Bot. [online] Available from: https://scholar.google.com/scholar?hl=es&as_sdt=0,3&cluster=7639530605626000306, 1994.

Zhang, Y., Aradottir, A. L., Serpe, M. and Boeken, B.: Interactions of Biological Soil Crusts with Vascular Plants, in Biological Soil Crusts: An Organizing Principle in Drylands, pp. 385–406., 2016.

Zhang, Y. M., Wu, N., Zhang, B. C. and Zhang, J.: Species composition, distribution patterns and ecological functions of biological soil crusts in the Gurbantunggut Desert, J. Arid Land, 2(3), 180–189, doi:10.3724/SP.J.1227.2010.00180, 2010.

Tables

Table 1: Chemical characteristics of the soil treatments. Different letters show statistical significance.

Treatment	Biopedtutbation soil			Underlying soil			BSC			*P*-value
	Mean	SEM		Mean	SEM		Mean	SEM		
EC dS/m (1:1)	1.99[a]	±	0.50	0.67[b]	±	0.34	0.40[b]	±	0.08	0.043*
$CaCO_3$ %	4.67[a]	±	0.67	2.02[b]	±	0.39	2.45[b]	±	0.31	0.043*
pH (1:1)	8.53	±	0.15	8.53	±	0.44	8.27	±	0.08	0.165
OM%	0.27[a]	±	0.13	0.38[a]	±	0.05	0.67[b]	±	0.08	0.043*
K (ppm)	242.00	±	6.00	379.33	±	13.61	428.67	±	99.93	0.165

P (ppm)	30.30	±	6.91	22.53	±	2.94	30.77	±	2.17	0.165

(*) Significant values, $p<0.05$. Median test for two independent medians.

Table 2: Plant density (ind/m^2) of paired soil treatments in seedbank germination experiment and seedlings emergence observations.

Species	Seedbank germination experiment				Seedlings emergence observations			
	BSC	Active	BSC	Inactive	BSC	Active	BSC	Inactive
Cistanthe paniculata	2311.1	603.7	2408.8	1564.7	67.4	118.8	52.8	50.0
Fuertesimalva peruviana	137.0	318.5	229.4	155.9	23.6	88.2	21.5	72.2
Chenopodium petiolare	25.9	18.5	394.1	70.6	-	-	-	-
Cryptantha limensis	0.0	14.8	147.1	61.8	0.7	2.1	0.0	6.3
Calandrinia alba	3.7	3.7	79.4	91.2	0.0	0.7	0.0	2.1
Nolana humifusa	103.7	18.5	20.6	38.2	0.0	2.1	0.0	4.2
Solanum phyllanthum	0.0	3.7	2.9	79.4	0.0	0.7	0.0	3.5

Oxalis lomana	81.5	14.8	0.0	5.9	-	-	-	-
Exodeconus prostratus	0.0	14.8	5.9	11.8	0.0	0.0	0.0	0.7
Palaua rhombifolia	11.1	0.0	14.7	14.7	0.0	0.7	0.0	0.7
Fuertesimalva limensis	37.0	3.7	2.9	0.0	-	-	-	-
Stenomesson coccineum	3.3	0.0	2.9		-	.	.	
Solanum multifidum	1.6	0.0	0.0		-	-	-	

Figures

Figure 1: Study area in the Coastal desert of Peru.

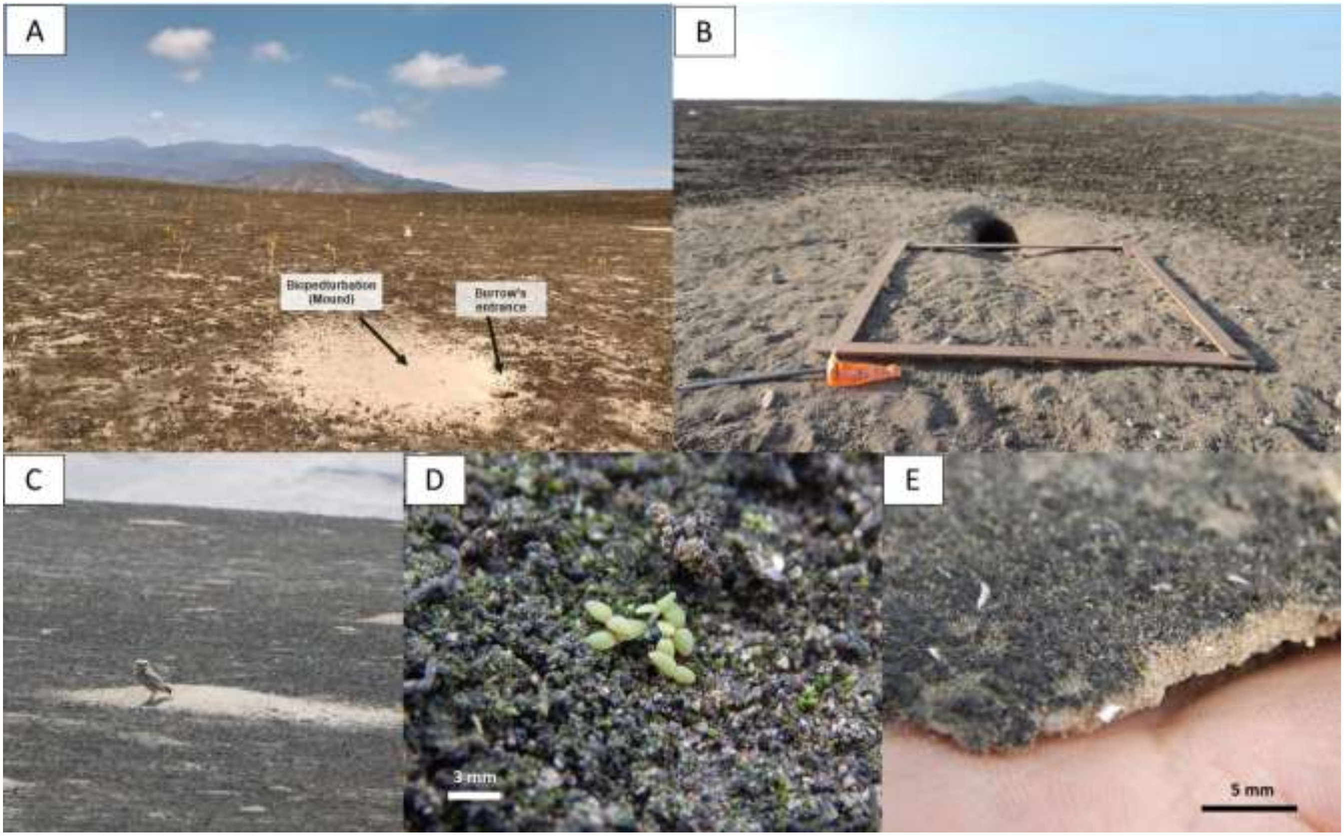

Figure 2. **A.** Landscape of the study area. The lower site of the hills, about 200 m above sea level, has a total surface cover of BSC except where it is disturbed by fossorial birds' burrows (Biopedturbation labeled in the picture). **B.** Biopedturbation studied, a 30x30 cm plot in the mound placed to observe seedling emergence. **C.** Burrowing owl *Athene cunicularia* standing on its biopedturbation. **D.** *Cistanthe paniculata* seedlings growing on BSC. **E.** Dark cyanobacterial biological soil crust that covers the study site.

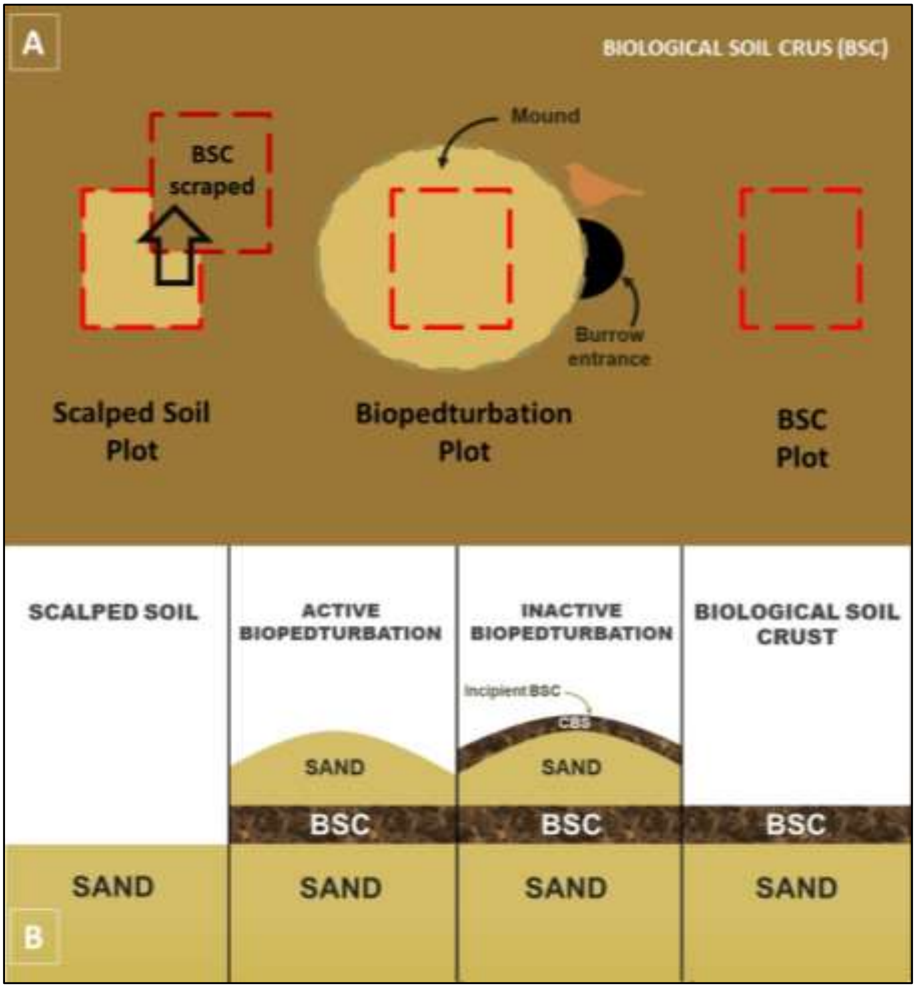

Figure 3. **A.** Soil moisture content experimental design. Three plots were stablished in active and inactive biopedturbations: Scalped soil, Biopedturbation and BSC plot. **B.** Four soil surfaces were sampled, each with a particular soil profile.

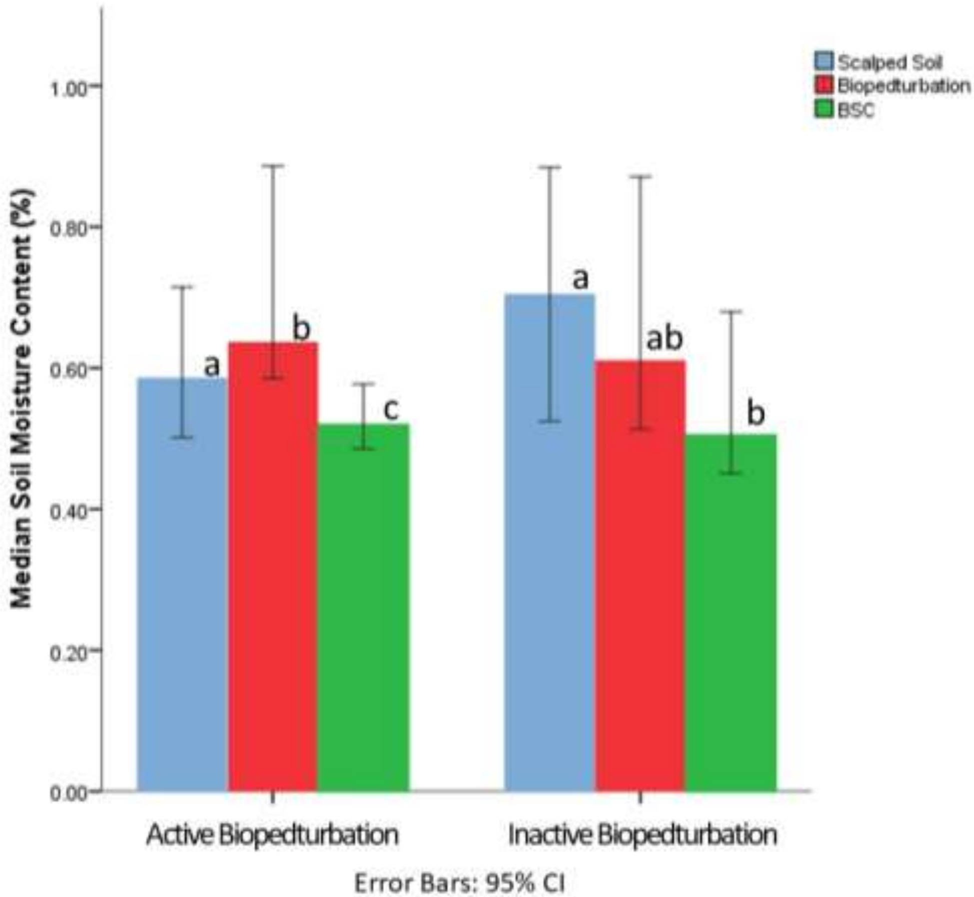

Figure 4: Soil moisture content (%) of the two types of biopedturbations (Median ± 95% intervals). Different letters indicate significant differences (Wilcoxon signed rank test; P< 0.05)

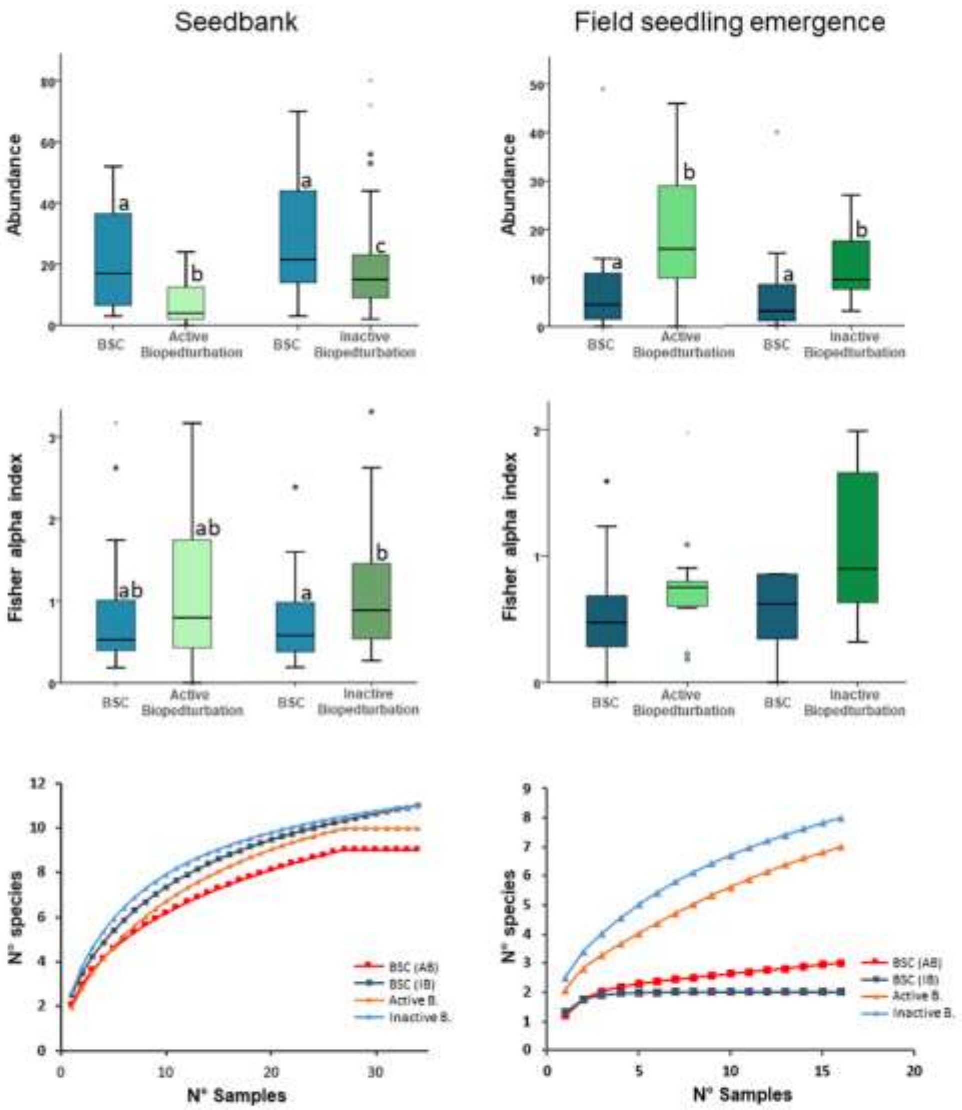

Figure 5: Seed bank and field seedling emergence. Abundance, diversity Fisher alpha index and rarefaction curve of paired treatments of biopedturbation and BSC. Different superscripts indicate a significant difference between BSC and active or inactive disturbance at P < 0.05. AB: Active Biopedturbation. IB: Inactive Biopedturbation.