RESEARCH ARTICLE

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Functional diversity of experimental annual plant assemblages drives plant responses to biological soil crusts in gypsum systems

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Abstract

1. Biological soil crusts (BSC) are complex biotic aggregates comprised of lichens, cyanobacteria, algae and other micro-organism that are known to differently affect plant development along life cycle by selecting plant functional traits based on species-specific effects. In addition, functional differences between interacting species should modulate their response ability to other environmental factors. Thus, it should be expected that the effects of the BSC on plants will be significantly determined by the own functional diversity in the community.

2. To understand the multiple effects of BSC and the extent to which the functional diversity of interacting plant species can modulate their effects on the development of coexisting species, we applied an experimental approach by manipulating the initial functional diversity of the entire annual plant community and BSC conditions in a common garden trial. We crossed three sorts of assemblages built on the basis of plant stature (combinations of only large, or only small, or diverse sized plant species in pots) with three lichen-dominated BSC disturbance scenarios (intact, or tiny mechanically disaggregated, or absent portions of BSC).

3. BSC strongly affected the establishment and development of gypsophilous annual plants in a complex, multifaceted manner, which shifted throughout the plant life cycle. We demonstrated that lichen-dominated BSC could act as a major physical barrier to the establishment of annual plants at a heterogeneous fine spatial scale. Such a restrictive effect was particularly marked in the presence of intact BSC. However, after annual plants overcame the restrictions imposed by BSC, the same biotic layer facilitated plant growth and fitness, regardless of its physical integrity, resulting in larger plants producing more fruits.

4. Importantly, our results suggest that the functional diversity structure of the community may also drive growth and fitness of coexisting species by activating alternative coexistence mechanisms such as niche partitioning or competition symmetry. This study highlights the importance of plant neighbourhood

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features for the performance of interacting species, and confirms a novel, experimental way to explore the effects of community diversity on plants for the interpretation of assembly mechanisms.

1 | INTRODUCTION

Understanding the processes that govern plant coexistence and community assembly is still a hot topic in plant ecology studies. According to the theory of species coexistence (Götzenberger et al., 2012; HilleRisLambers et al., 2012; Keddy, 1992), the composition of a local plant community is determined by any ecological process that selects for or against species from the regional species pool. Assembly rules act hierarchically at different biological and geographical scales via organism dispersion, the abiotic environment and biotic interactions (Götzenberger et al., 2012) to ultimately determine the participation and performance of species in the realized community. A representative example of a biotic component that greatly affects plant assembly processes is the biological soil crust (BSC), a complex combination of lichens, cyanobacteria, mosses, algae, fungi and microarthropods that are intimately associated with particles on or within the top few centimetres of the soil surface (Belnap et al., 2016). These soil communities are widely distributed in drylands worldwide (e.g. Rodriguez-Caballero et al., 2018) due to the tolerance of some of their components to extreme temperatures, drought and solar radiation (Belnap, 2003). Considering that drylands cover about 41% of the Earth's land surface (Safriel et al., 2005), BSC are important features of terrestrial systems (Belnap et al., 2016), where they comprise a living layer that can substantially affect the establishment and development of plants.

Several studies have highlighted the importance of BSC in the functioning of semi-arid environments since biocrusts can modulate crucial processes here, such as soil water infiltration and evapotranspiration (Berdugo et al., 2014; Chamizo et al., 2012; Maestre et al., 2002), the carbon cycle (Bowker et al., 2010; Maestre & Cortina, 2003), nitrogen fixation (Belnap, 2002; Elbert et al., 2012; Harper & Belnap, 2001), nitrification (Castillo-Monroy et al., 2010; Delgado-Baquerizo et al., 2010), soil stabilization and sediment trapping (Chaudhary et al., 2009), soil enzyme activities (Bowker et al., 2011) and litter decomposition (Berdugo et al., 2021). On semi-arid gypsum soils, lichens are the dominant components of BSC (Maestre et al., 2011, 2021) and can form a hard crust, which may be highly resistant to root penetration (e.g. *Diploschistes*; Escudero et al., 2007), thereby imposing a physical barrier to many plant species (Escudero et al., 2007; Meyer, 1986; Romão & Escudero, 2005). In addition, some lichens in BSC can produce secondary metabolites with inhibitory effects on seed germination and seedling growth by vascular plants (Favero-Longo & Piervittori, 2010; Rundel, 1978). Studies have shown that these interactions between vascular plants

and BSC-forming lichens can be highly species specific (Escudero et al., 2007; Maestre et al., 2011). In gypsum systems, BSC can affect several phases of annual plant life cycles (e.g. seed bank formation, Peralta et al., 2016; seed germination and seedling establishment, Escudero et al., 2007; and plant development and the phenological peak, Luzuriaga et al., 2012, 2015). Peralta et al. (2019) and Sánchez et al. (2022) demonstrated the complex, multifaceted physical effects of BSC on annual plant assemblages. They found that intact BSC negatively affected seed germination and seedling establishment while in later stages BSC buffered adverse abiotic conditions. Many of the effects of BSC on plant development and fitness are still unclear and poorly understood (e.g. Maestre et al., 2021).

Another important aspect is the functional diversity (FD) in the community, which has received much attention by observational studies to infer assembly forces and mechanisms (Grime, 2006; Lavorel & Garnier, 2002; McGill et al., 2006; Shipley, 2010). For instance, lower functional diversity than expected by chance, or functional convergence of the community (Weiher et al., 2011), may result from intense abiotic environmental stressful conditions selecting for species with functional traits that are best adapted to an environment (Funk et al., 2017). By contrast, when plant–plant competition is the main restrictive force, coexisting species may exhibit more diverse functional strategies than expected by chance, or functional divergence, due to limiting similarity (Funk et al., 2017; Weiher et al., 2011). To confirm, however, these causal relationships, the responses of participant species to FD patterns in the community should be explored. In this study, we aimed to understand the effect of the functional structure of the plant assemblage itself (functional convergence vs. divergence) on the performance of coexisting species in terms of survival, growth and fitness. To the best of our knowledge, very few studies have manipulated the initial FD to assess causality in the community assembly process (but see Feng et al., 2019; Galland et al., 2019; Schittko et al., 2014). Indeed, Chaves et al. (2021), using phylogenetic relatedness among species as a proxy of FD in experimental assemblages, have recently shown niche complementarity (i.e. functional divergence attenuating competition) as a major mechanism of species coexistence in annual plant communities in gypsum systems. Understanding how the functional structure of a plant assemblage interacts with BSC to lead to differences in plant performance and reproductive success would represent a significant, novel advance in the comprehension of the assembly process.

The main objective of this study was to determine the effects of BSC combined with the initial FD of species assemblages in

terms of the maximum plant height (MPH), on plant development and fitness of the coexisting species. We prepared experimental assemblages of annual plants with initial high FD (i.e. coexisting species with different maximum sizes, which we refer to as the mixed sized scenario) and low initial FD (i.e. coexisting species only with large or small maximum sizes, which we refer to as the large- and small-sized scenarios, respectively). We selected the MPH to manipulate the FD in assemblages because this trait has been reported to be sensitive to the physical integrity of the BSC in annual plant assemblages in our study systems (Peralta et al., 2019; Sánchez et al., 2022). Furthermore, the MPH is known to strongly determine the competitive ability of plant species (Garnier et al., 2016), and thus this trait may be crucial during the peak of vegetation development when strong competitive interactions are expected to occur among adult plants. To detect the effects of the BSC, we tested three levels of biocrust disturbance: (i) intact portions of BSC; (ii) disaggregated, tiny fractions of BSC representing disturbed dryland soils, where BSC physical effects should be attenuated (Peralta et al., 2019); and (iii) bare soil to eliminate any effect of the BSC.

We hypothesized that the effect of BSC would shift depending on the life cycle phase of annual plants on gypsum drylands, which would also be modulated by the FD of the plant assemblage itself. In particular, we tested two hypotheses. First, we hypothesized that the restrictive effect of the BSC would result in lower plant abundance, especially with the intact BSC and to a lesser extent with the disaggregated BSC. Indeed, we expected that the restriction on the establishment of plants would be exacerbated in small-sized species because BSC are usually detrimental to the emergence of small plants (Peralta et al., 2019). In contrast, in late life stages, we expected that the amelioration of the microenvironmental conditions mediated by BSC would promote plant growth and fitness (Belnap, 2003; Boeken, 2008). This facilitative effect would be more pronounced with intact BSC, because all ameliorating properties are retained, and would also depend on initial FD, as next postulated. Second, if niche complementarity is a major driver of plant coexistence in these gypsum annual plant communities, as recently suggested by Chaves et al. (2021), and plant stature is involved in their competitive hierarchies, then plants in functionally diverse assemblages (i.e. mixed plant sized scenarios) should grow and reproduce better than those in species combinations with low functional diversities (i.e. small or large plant sized scenarios), because we expect that in functionally diverse plant sized scenarios competition intensity among coexisting species would be less than in functionally low diverse ones.

2 | MATERIALS AND METHODS

2.1 | Target community

The experimental system comprised the prolific ephemeral communities of annual plants that live on gypsum soils in the central Tagus Valley, central Spain. The presence of large amounts of gypsum (calcium sulphate dihydrate, CaSO4·2H2O) leads to stressful physical and chemical soil properties for plant life (i.e. high mechanical instability, low soil porosity, extreme nutritional deficits, high concentration of sulphates and moderate salinity; Escudero et al., 2015; Guerrero-Campo et al., 1999). The climate in the study area is semi-arid Mediterranean with a mean annual temperature of 15°C (ranging between average values of 33.2°C and 1.2°C in the warmest and coldest months of July and January, respectively) and mean annual rainfall of 365 mm m^{-2} year^{-1} (Getafe weather station, 40°17′58′′N; 3°43′20′′E; 620 m). Precipitation is concentrated in the late autumn and early spring, with an intense summer drought. Tussock grasses comprising *Macrochloa tenacissima* (L.) Kunth. and sparse, patchily distributed gypsophilous dwarf shrubs (e.g. *Lepidium subulatum* L., *Centaurea hyssopifolia* Vahl., *Gypsophila struthium* L. and *Helianthemum squamatum* (L.) Dum. Cours.) dominate the above-ground vegetation. Furthermore, the gypsum soils have a well-developed BSC in open soil areas, which mostly comprise lichens (e.g. *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (G.H. Weber) Poelt, *Fulgensia subbracteata* (Nyl.) Poelt, *Toninia sedifolia* (Scop.) Timdal and *Psora decipiens* (Hedw.) Hoffm). BSC usually coexist with ephemeral highly dense annual plant communities (up to 38 species/0.25 m^2) formed from a rich regional species pool (around 120 species; e.g. *Chaenorhinum reyesii* (C. Vicioso & Pau) Benedí, *Festuca gypsophila* (Hack.) Paunero, *Campanula fastigiata* Dufour ex Schult., *Alyssum simplex* Rudolphi, *Cerastium glomeratum* Thuill., *Filago pyramidata* L. and *Reseda stricta* Pers.; Luzuriaga et al., 2012, 2015, 2018). The life cycles of these annual plant species are short and highly synchronized, with two seed germination peaks at the end of the autumn rains (around October) and the end of the early spring rains (around February). Seed dispersal by most species occurs in May and June (Luzuriaga et al., 2012).

2.2 | Collection of BSC and seeds for the experimental setup

The BSC portions used in the experiments comprised the intact thallus of the crustose lichen *D. diacapsis* and foliose lichen *S. lentigera*, which were the two dominant representative components of the BSC in our study system (Luzuriaga et al., 2012). In June 2019, we collected BSC portions using a wide sheet knife and carefully cleaned adhered soil particles by means of a toothbrush while trying to maintain their physical integrity. To avoid the natural retention of seeds in small BSC fissures, we extended them on plastic draining trays in a greenhouse with a thermal control system. During the first 2 weeks, the temperature inside the greenhouse was kept at 40–50°C to induce heat shock in the seeds, which is known to effectively break seed dormancy in our system (see Luzuriaga et al., 2012). The greenhouse temperature was then stabilized at 20°C and trays were regularly watered for 3 months to promote germination of the seeds retained in the BSC samples. Emergent seedlings were manually removed immediately after detection to ensure that the BSC portions used in the experiment were free of seeds.

In addition, we collected seeds from up to 40 apparently healthy random individuals of each of 23 annual plant species (see Table 1

for the complete species list). We collected seeds during May–June 2017 and 2018 at three locations in the central Tagus valley with similar geographical and climatic conditions: Aranjuez (40°02′11.7″N, 3°32′59.5″W; 591 m), Ciempozuelos (40°08′36.9″N, 3°37′00.0″W; 585 m) and Portalrubio de Guadamejud (40°17′34.4″N, 2°35′31.0″W; 755 m). Seeds were cleaned and stored in paper envelopes in a dry environment in the laboratory until September 2019. Before sowing (October 2019), seeds were subjected to a light thermal heat shock (15 days at 50°C) to break seed dormancy.

2.3 | Experimental design

We conducted a factorial experiment at the CULTIVE facilities of Rey Juan Carlos University (Móstoles, Spain; https://urjc-cultive.webnode.es/) from October 2019 to June 2020. We performed a common garden experiment by crossing three FD scenarios in terms of the MPH trait and three BSC disturbance levels (Figure 1). We defined MPH as the shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level

TABLE 1 Complete list of species used in the experiment, grouped by functional scenarios built based on the trait maximum plant height (MPH) and labelled alphabetically: A and B correspond to highly diverse scenarios of mixed sized species; C and D to low diverse scenarios of small sized species; E and F to low diverse scenarios of large-sized species. For each experimental species, the value of the species MPH and the corresponding botanic family are shown. Mean MPH and the initial Rao $_{MPH}$ (see methods) for each functional scenario are also indicated. [Correction added on 12 December 2022, after first online publication: Table 1 has been revised]

Species	Family	MPH (cm)	Scenario
Bombycilaena discolor (Pers.) M. Laínz.	Asteraceae	8.12	A
Bupleurum semicompositum L.	Apiaceae	8.76	**Mean MPH**
Centaurea melitensis L.	Asteraceae	28.29	11.23 cm
Neatostema apulum (L.) I.I.Johnst.	Boraginaceae	9.50	**Rao** $_{MPH}$
Plantago afra L.	Plantaginaceae	3.99	1.44
Ziziphora hispanica L.	Lamiaceae	8.70	
Alyssum simplex Rudolphi	Brassicaceae	2.59	B
Asterolinon Linum-stellatum (L.) Duby.	Primulaceae	2.33	**Mean MPH**
Eruca vesicaria (L.) Cav.	Brassicaceae	19.23	10.13 cm
Galium parisiense L.	Rubiaceae	17.77	**Rao** $_{MPH}$
Pistorinia hispanica (L.) DC.	Crassulaceae	7.77	1.03
Stoibrax dichotomum (L.) Raf.	Apiaceae	11.09	
Asterolinon Linum-stellatum (L.) Duby.	Primulaceae	2.33	C
Echinaria capitata (L.) Desf.	Poaceae	3.70	**Mean MPH**
Filago pyramidata L.	Asteraceae	5.71	6.61 cm
Neatostema apulum (L.) I.I.Johnst.	Boraginaceae	9.50	**Rao** $_{MPH}$
Lomelosia stellata (L.) Raf.	Caprifoliaceae	9.74	0.20
Ziziphora hispanica L.	Lamiaceae	8.70	
Alyssum simplex Rudolphi	Brassicaceae	2.59	D
Bombycilaena discolour (Pers.) M. Laínz.	Asteraceae	8.12	**Mean MPH**
Bupleurum semicompositum L.	Apiaceae	8.76	6.68 cm
Hedypnois cretica (L.) Dum-Cours.	Asteraceae	8.82	**Rao** $_{MPH}$
Pistorinia hispanica (L.) DC.	Crassulaceae	7.77	0.14
Plantago afra L.	Plantaginaceae	3.99	
Astragalus stella L.	Fabaceae	13.19	E
Bromus rubens L.	Poaceae	12.94	**Mean MPH**
Galium parisiense L.	Rubiaceae	17.77	13.31 cm
Limonium echioides (L.) Mill.	Plumbaginaceae	10.23	**Rao** $_{MPH}$
Malva aegyptia L.	Malvaceae	14.64	0.14
Stoibrax dichotomum (L.) Raf.	Apiaceae	11.09	
Asteriscus aquaticus (L.) Less	Asteraceae	16.21	F
Biscutella auriculata L.	Brassicaceae	23.45	**Mean MPH**
Eruca vesicaria (L.) Cav.	Brassicaceae	19.23	17.67 cm
Galium parisiense L.	Rubiaceae	17.77	**Rao** $_{MPH}$
Malva aegyptia L.	Malvaceae	14.64	0.22
Torilis nodosa (L.) Gaertn.	Apiaceae	14.74	

(Cornelissen et al., 2003). MPH was applied as a key functional trait in our community model because (i) previous studies of these plant communities identified MPH as a functional trait that is particularly sensitive to BSC (Peralta et al., 2019), where large-sized plants were more successful in the establishment phase than small-sized plants when BSC remained intact; and (ii) MPH can represent the competitive ability of a species (Garnier et al., 2016; King, 1990; Westoby et al., 2002), and thus it is expected to have a crucial effect on the assembly dynamics of rapid life-cycle organisms with dense distributions (i.e. patches of annual plants) during the life phases following emergence. We recognize that the concept of functional diversity may be wider than just the variability in one trait, but the core role that MPH seem to play in the organization of annual plant communities in semiarid environments, would make the manipulation of this trait a good proxy of changes in the functional structure of the assemblage.

We prepared three FD scenarios based on the MPH trait: (1) all coexisting species had large maximum heights, (2) all coexisting species had small maximum heights and (3) coexisting species had a wide range of MPH values, that is, large, small and mixed sized species scenarios, respectively. All MPH values were estimated for our species based on measurements of at least 10 healthy individuals per species collected randomly in the study area, according to the protocols defined by Cornelissen et al. (2003). To control for the idiosyncratic effects of species identities, we prepared two different combinations of species for each functional scenario (Figure 1; details of the species in each experimental assemblage are given in Table 1). Each combination comprised six species (20 seeds per species). To achieve the experimental contrasting FD values among assemblages, we selected species combinations defined by their Rao's quadratic entropy index (Botta-Dukát, 2005), calculated on the basis of the species MPH distances by the following formula:

$$\text{Rao}_{\text{MPH}} = \sum d_{ij}\, p_i p_j,$$

where i and j represent different species, respectively, d denotes the Euclidean distance between i and j in terms of the MPH value, and p represents the proportion of each species in the assemblage. In the calculation, we considered a relative species abundance of 20 individuals for all the six participant species in each assemblage (i.e. the number of seeds sown in each pot per species; see Table 1 for resulting Rao $_{\text{MPH}}$ values in assemblages). We calculated Rao indexes by the *dbFD* function in the ꜰᴅ package (Laliberté et al., 2014; Laliberté & Legendre, 2010).

The BSC disturbance levels comprised: (1) intact portions of BSC, (2) disaggregated BSC produced by mechanical disaggregation of the BSC with a mallet (the BSC was spread over the pot soil as small

(a) Schematic illustration of the experimental design
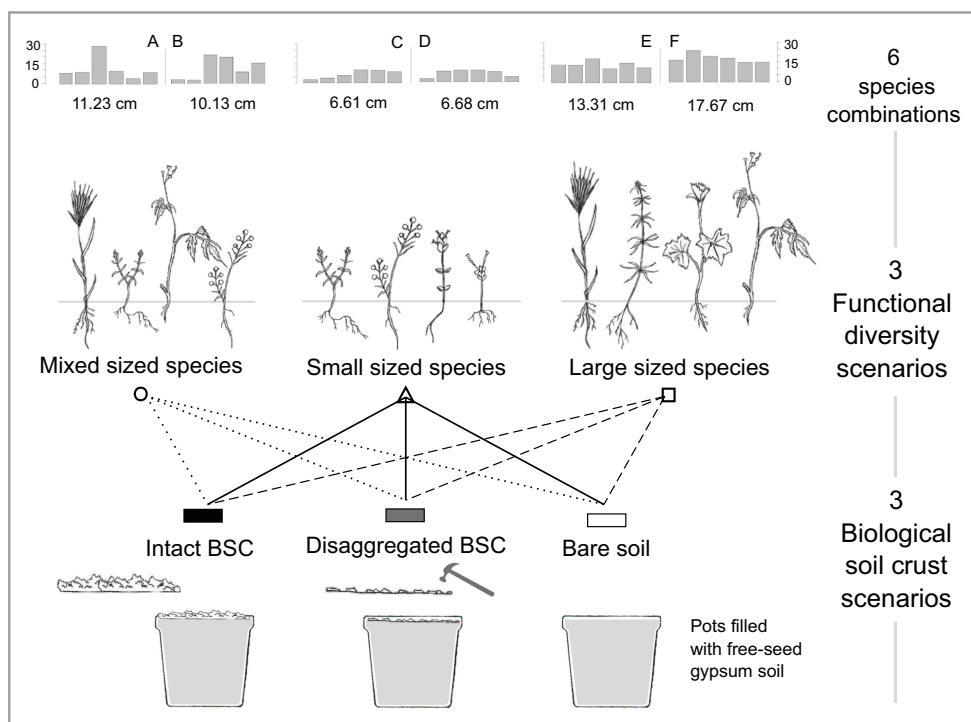
(b) Photos of the experimental setup

FIGURE 1 (a) Schematic illustration of the experimental design. We designed three functional diversity scenarios, with initial assemblages formed by species with a wide range of maximum plant heights (MPH; mixed sized species), or only by small- or large-sized species, each with two combinations of six species (a, b for species with different sizes; c, d for small species; e, f for large species). Bars in the top graphics represent the individual species sizes (MPH in cm) in each combination, with the average for each group shown below. We tested the effects of a biological soil crust (BSC) on these species assemblages by combining them with three BSC disturbance scenarios (intact, disaggregated BSC and bare soil). The 18 resulting treatment combinations were replicated 15 times (=270 pots). (b) Photos of the experimental setup in the greenhouse showing details of the experimental biological soil crust (up) and the experimental realized assemblages (down).

TABLE 2 Generalized linear models (GLM) to explore changes in plant abundance, plant growth and fruit production of each specie per pot. We classified our species into two groups: (a) species present only in one initial functional diversity scenario (mixed, or small-, or large-sized species), and b) species present in two initial functional diversity scenarios (mixed plus small-or plus large-sized species). In the group (a), the biological soil crust treatment (BSC) was included in the model as a fixed factor, while in the group (b), besides BSC we also included the initial functional diversity scenario (FD) and their interaction as fixed factors. The error distribution and the link function to model each plant variable are indicated in the table head. Type III Wald chi-square tests were performed to estimate significance. df = degrees of freedom. Significant results are shown in bold and indicated with asterisks: ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$

(a) Species present only in one initial FD scenario

			Plant abundance	Plant growth	Number of fruits
		Error distr.	Poisson	Gaussian	Gamma
		Link	log	Identity	Inverse
Species		df	Wald Chisq	Wald Chisq	Wald Chisq
Asteriscus aquaticus	BSC	2	**12.942****	**24.271*****	5.611
Astragalus stella	BSC	2	4.377	**19.389*****	1.706
Biscutella auriculata	BSC	2	**21.105*****	**13.714****	na
Bromus rubens	BSC	2	**7.153***	**9.673****	**99.786*****
Centaurea melitensis	BSC	2	4.18	**17.3*****	**9.82****
Echinaria capitata	BSC	2	1.731	**15.874*****	**69.65*****
Filago pyramidata	BSC	2	**9.953****	**38.977*****	**30.825*****
Hedypnois cretica	BSC	2	**14.26*****	**14.08*****	**49.672*****
Limonium echioides	BSC	2	4.177	na	na
Lomelosia stellata	BSC	2	**6.248***	4.991	**19.48*****
Malva aegyptia	BSC	2	**19.776*****	**30.591*****	**11.617****
Torilis nodosa	BSC	2	0.654	**100.27*****	**61.209*****

(b) Species present in two initial FD scenarios

			Plant abundance	Plant growth	Number of fruits
		Error distr.	Poisson	Gaussian	Gamma
		Link	log	Identity	Inverse
Species		df	Wald Chisq	Wald Chisq	Wald Chisq
Alyssum simplex	BSC	2	4.686	4.584	**8.61***
	FD	1	0.252	0.397	0.011
	BSC×FD	2	0.591	0.473	1.119
Asterolinon Linum-stellatum	BSC	2	3.658	**85.713*****	**197.186*****
	FD	1	**15.715*****	**8.094****	**73.944*****
	BSC×FD	2	1.921	0.348	**20.677*****
Bombycilaena discolor	BSC	2	0.093	**17.643*****	**90.964*****
	FD	1	**9.608****	0.377	1.5
	BSC×FD	2	2.797	0.395	2.994
Bupleurum semicompositum	BSC	2	1.707	**57.018*****	**45.539*****
	FD	1	2.285	2.341	0.357
	BSC×FD	2	3.624	**14.241*****	0.564
Eruca vesicaria	BSC	2	**6.514***	1.256	na
	FD	1	1.697	**11.030*****	na
	BSC×FD	2	**6.591***	5.546	na

(Continues)

TABLE 2 (Continued)

(b) Species present in two initial FD scenarios

Species		Error distr. Link df	Plant abundance Poisson log Wald Chisq	Plant growth Gaussian Identity Wald Chisq	Number of fruits Gamma Inverse Wald Chisq
Galium parisiense	BSC	2	1.652	30.699***	15.08***
	FD	1	16.447***	1.724	11.077**
	BSC×FD	2	0.939	3.082	3.367
Neatostema apulum	BSC	2	13.985***	29.564***	39.957***
	FD	1	0.313	0.625	52.61***
	BSC×FD	2	1.977	0.046	2.831
Plantago afra	BSC	2	6.741*	9.684**	68.378***
	FD	1	1.415	0.117	0.186
	BSC×FD	2	2.349	17.845***	1.256
Pistorinia hispanica	BSC	2	0.611	15.066***	na
	FD	1	7.483**	0.502	na
	BSC×FD	2	2.458	2.597	na
Stoibrax dichotomum	BSC	2	1.902	30.981***	3.857
	FD	1	0.038	0.000	3.858*
	BSC×FD	2	0.087	2.167	0.157
Ziziphora hispanica	BSC	2	14.51***	129.887***	70.375***
	FD	1	0.863	1.299	2.697
	BSC×FD	2	3.444	4.732	1.624

fragments and dust) and (3) bare soil without BSC. The intact and disaggregated BSC scenarios were produced by mixing *D. diacapsis* and *S. lentigera* thallus pieces free of seeds in similar proportions. Our BSC experimental material was somewhat simplified, but it was a reasonable representation of the natural BSC found in our study system in semiarid gypsisol systems in the Tagus valley. Therefore, our factorial design comprised: three BSC levels × three plant FD levels × two species combinations = 18 scenarios. Each scenario was replicated 15 times, thereby resulting in 270 experimental assemblages (pots; Figure 1).

The experimental pots were square with a capacity of 6 L (21 cm width × 21.6 cm height). The pots were filled with seed-free gypsum soil from a gypsum quarry located near the biological material collection sites. In September 2019, each pot was randomly assigned to one of the three BSC treatments. On the top of each pot, we manually placed intact portions of BSC, tiny fractions of previously disaggregated BSC, or left the soil bare (intact BSC, disaggregated BSC and bare soil treatments, respectively). In October 2019, we sowed 20 seeds from each six species to form each functional combination (i.e. a mix of 120 seeds) per pot, with 15 pots for each BSC × MPH scenario × species combination. Irrigation was provided manually to the soil water-carrying capacity once each week to remove any water restriction in the pots, thereby ensuring that we only tested the effects of BSC on the assemblages. The effects of the treatments on the soil moisture levels were recorded in two pots per treatment with a time domain reflectometer at 5 cm of soil depth (model TDR 100, Campbell

Scientific), and we found no differences between treatments, except for small differences in December and January between the bare soil and intact BSC pots (see Appendix S1).

## 2.4 | Sampling of experimental communities

We recorded plant abundance as the number of individuals of each species that emerged in each pot in the plant development peak (March 2020). We measured the vegetative stem height of the tallest individual per species in each pot as an estimate of the plant growth at the development peak. In addition, the number of fruits produced per individual. In particular, we recorded the fruit number produced in 19 of our 23 experimental species because *Pistorinia hispanica* did not produce fruits and we were unable to record the number of fruits for *Eruca vesicaria*, *Biscutella auriculata*, and *Limonium echioides* due to the COVID-19 lockdown from March to May 2020 in Spain.
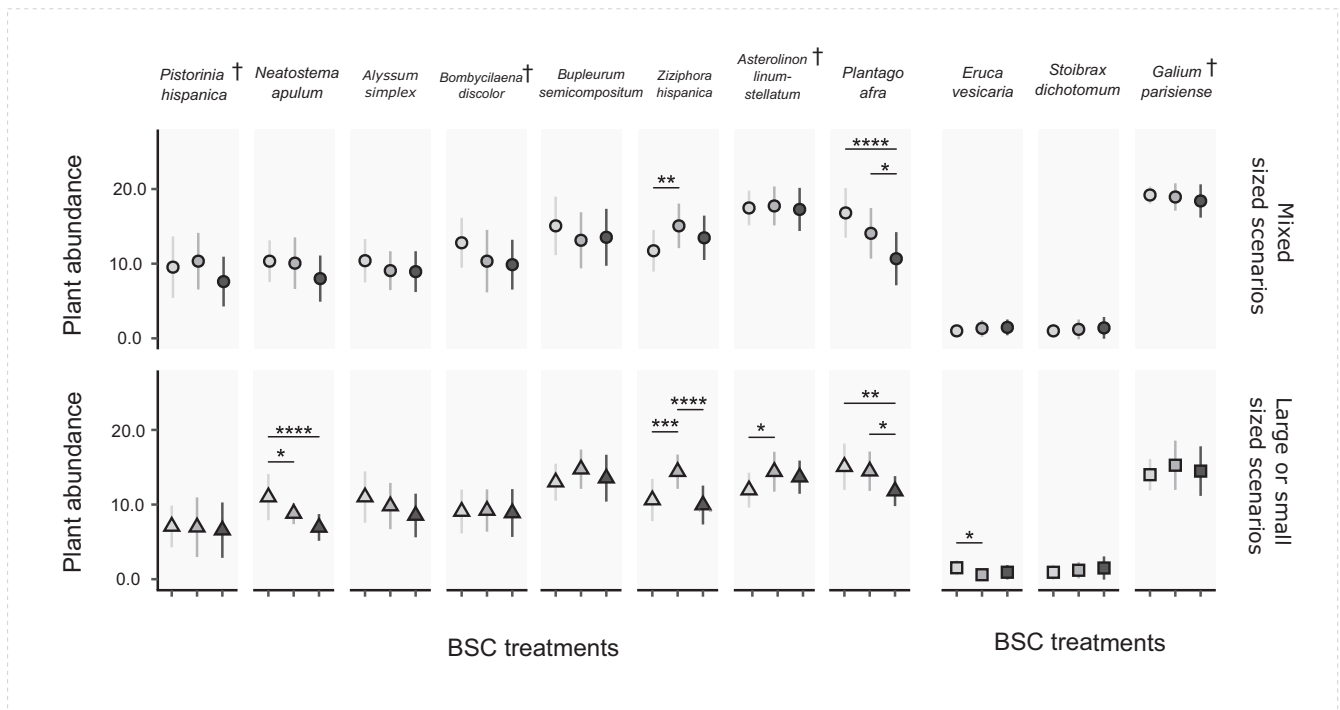
2.5 | Statistical analyses

2.5.1 | Plant abundance

We used generalized linear models (GLM) to analyse the effects of the BSC treatments and the initial functional diversity (FD) scenarios

(a) Species present only in one FD scenario
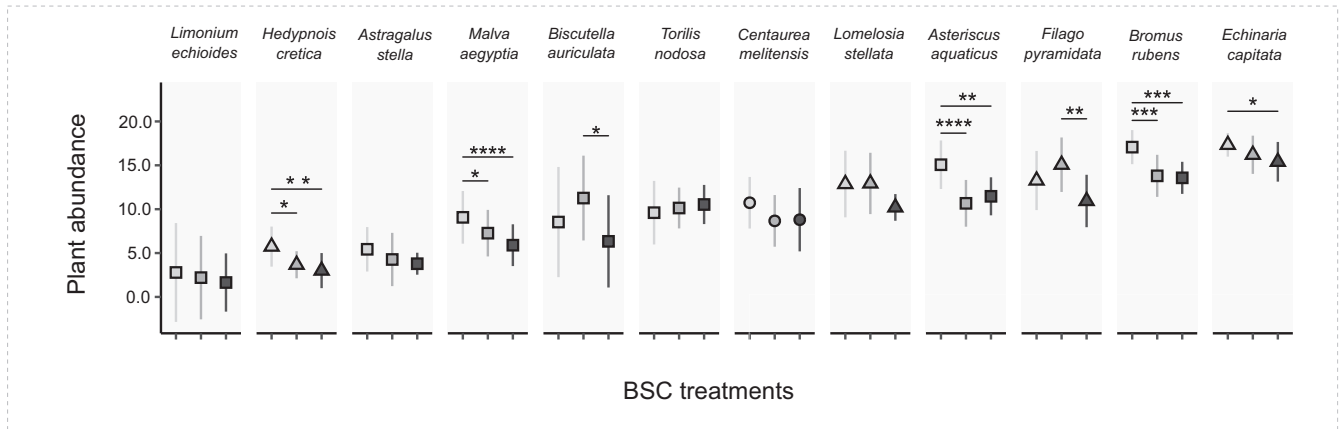
(b) Species present in two FD scenarios

* Symbol † next to the species name indicates significant differences between low and high initiall functional diversity scenarios: see statistical analyses in Appendix III.

FIGURE 2 Plant abundance per species at the vegetation development peak (March 2020; see Table 2 for the statistical models for all species). (a) Species present only in one initial functional diversity scenario (mixed, or small-sized, or large-sized species). (b) Species present in two initial functional diversity scenarios (mixed and small, or mixed and large-sized species). Vertical bars represent standard errors. We conducted post hoc Tukey's tests for differences between biological soil crust (BSC) treatments for each species. Horizontal bars above the mean values indicate pairs of cases responsible for significant differences and asterisks the level of significance: ****$p < 0.0001$; ***$p < 0.001$; **$p < 0.01$; *$p \leq 0.05$.

on the total plant abundance of each species per pot in March. We constructed 23 statistical models. Specifically, we modelized the plant abundance response of 12 species that occurred only in one FD scenario, where we included the BSC treatment (intact BSC, disaggregated BSC or bare soil) as a fixed factor; and that of 11 species that occurred in two initial FD scenarios (low and high FD), where we included the initial FD (large or small vs. mixed sized species) and BSC treatment as independent variables, and their interaction. We

used the Poisson distribution as the error distribution and log link function. We also performed post-hoc analyses to assess the differences in the total plant abundance.

2.5.2 | Plant growth and fruit production

We used GLM to explore the effects of the experimental treatments on each plant species growth, measured as the size of the tallest individual per pot, and on each species fruit production, measured as the mean number of fruits per fruiting plant (i.e. the total number of fruits/the number of fruiting plants) per each species and pot. We constructed 22 statistical models for plant growth, with one for each experimental species (except for *Limonium echioides* due to the lack of sufficient data). Specifically, we modelized the growth response of 11 species that occurred only in one FD scenario, where we included the BSC treatment as a fixed factor; and that of 11 species that occurred in two initial FD scenarios, where we included the initial FD and BSC treatment as independent variables, and their interaction. We used the Gaussian distribution as the error distribution and identity as the link function. We constructed 19 statistical models to evaluate fruit production, with one for each experimental species (except for *Pistorinia hispanica*, *Eruca vesicaria*, *Biscutella auriculata* and *Limonium echioides*, see above). Specifically, we modelled the fruiting response of 10 species that occurred only in one FD scenario, where we included the BSC treatment as a fixed factor; and that of nine species present in two initial FD scenarios, including the initial FD, BSC treatment and their interaction as independent variables. We used the Gamma distribution as the error distribution and inverse as the link function.

We used the *glm* function in the STATS package (R Core Team, 2021) to construct GLM. We performed Tukey HSD post-hoc tests with the *tukey_hsd* function in the RSTATIX package (Kassambara, 2021). All analyses were performed with R software version 4.0.5 (R Core Team, 2021).

3 | RESULTS

3.1 | Plant abundance

The BSC treatments significantly determined plant establishment in 11 out of 23 species (Table 2). Compared with bare soil, intact portions of BSC substantially reduced plant abundance in these 11 species, whereas the disaggregated BSC only had a slight restrictive effect on few species (Figure 2). The initial FD also affected plant

establishment in 4 out of 11 species, where more plants established in mixed sized scenarios than in low functional diversity scenarios (large or small; Table 2; Figure 2b).

3.2 | Plant growth and fruit production

We recorded 16,740 plants from our 23 experimental species and more than 180,000 fruits. Intact or disaggregated BSC strongly promoted the growth of plants (Table 2). In particular, most species (20 out of 22 with available data) were larger in the presence of the BSC (regardless of physical integrity) compared with bare soil (Figure 3). Plant growth of 4 out of 10 species (i.e. *Asterolinon linum-stellatum*, *Eruca vesicaria*, *Plantago afra* and *Bupleurum semicompositum*) was significantly affected by the initial FD of the species assemblage where they grew, where plants were larger under the low FD treatments (large- or small-sized scenarios) comparing with the high FD treatments (mixed sized scenarios; Figure 3b; Table 2b).
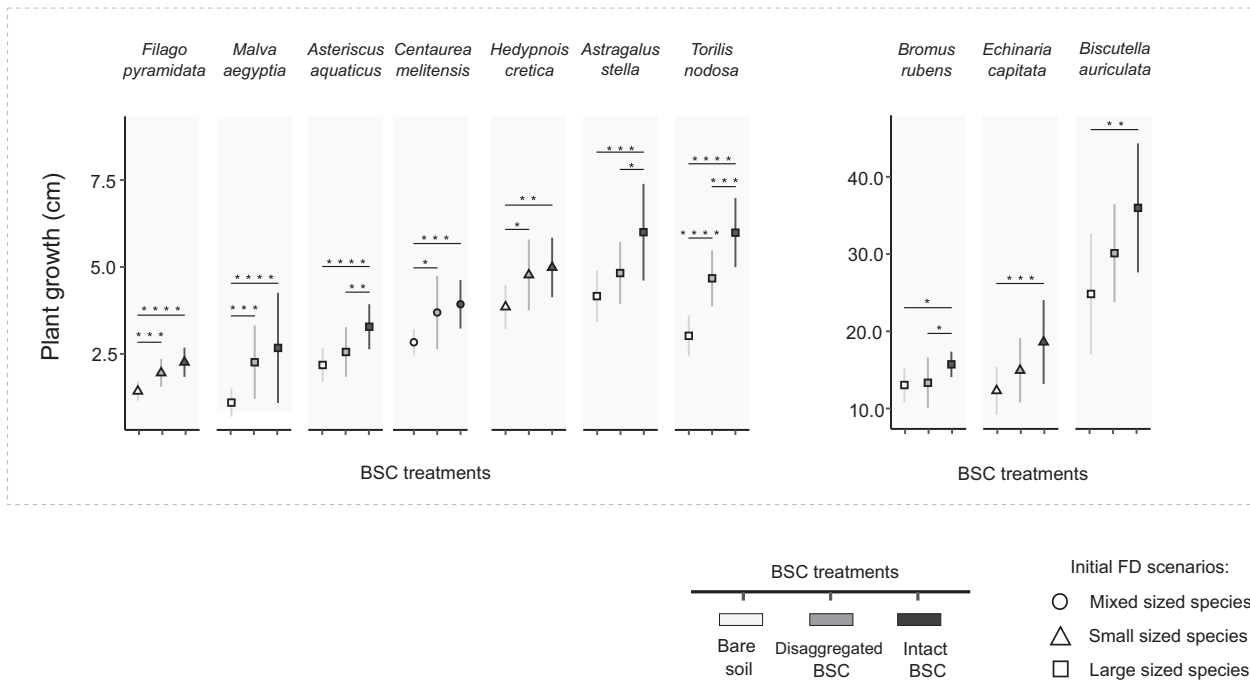
Fruit production per plant was similar under the intact and the disaggregated BSC treatments, where most species (16 out of 19 with available data) produced more fruits per plant with the presence of BSC (regardless of physical integrity) than in the bare soil scenarios (Figure 4; Table 2). The initial FD of the assemblage significantly affected fruit production in 4 out of 9 species that grew in two FD scenarios (i.e. *A. linum-stellatum*, *Galium parisiense*, *Neatostema apulum* and *Stoibrax dichotomum*). In these cases, species produced more fruits under the high FD scenarios (mixed sized species) than the low FD scenarios (small- or large-sized species; Figure 4b; Table 2b).
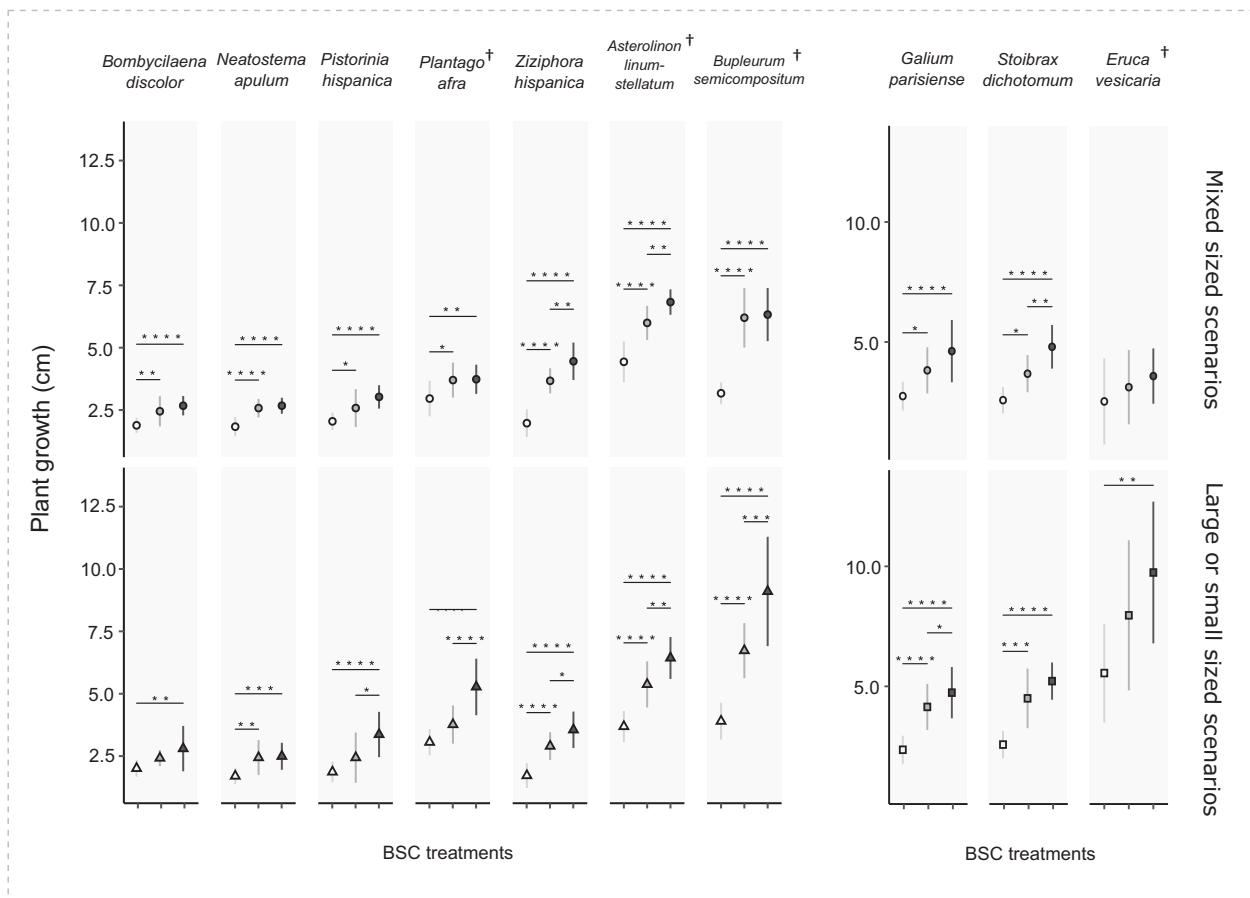
4 | DISCUSSION

The results obtained in this study largely agreed with our hypotheses. The lichen-dominated BSC strongly affected the establishment and development of gypsophilous annual plants in a complex, multifaceted manner, which varied throughout the plant life cycle. Overall, BSC-forming lichens presented a significant barrier that substantially restricted the establishment of plants, especially in the presence of intact BSC, but the same biotic layer appeared to facilitate plant growth and plant fitness (measured as the total number of fruits/the number of fruiting plants). In addition, the functional diversity of the experimental assemblages designed based on the MPH trait contributed to determine the plant performance of participant species. Niche complementarity may importantly operate on the organization of assemblages in these annual plant communities, since fitness of species (i.e. fruit production) increased with MPH

FIGURE 3 Mean plant growth measured as the vegetative stem height of the tallest individual per species in each pot at the vegetation development peak (March 2020). Species with significant differences between the biological soil crust (BSC) treatments or initial FD scenarios are presented (see Table 2 for statistical models for all species). (a) Species present only in one initial functional diversity scenario (mixed, or small-, or large-sized species), and (b) species present in two initial functional diversity scenarios (mixed and small, or mixed and large-sized species). Vertical bars represent standard errors. We conducted post hoc Tukey tests for differences between BSC treatments for each species. Horizontal bars above the mean values indicate pairs of cases responsible for significant differences and asterisks the level of significance: ****$p < 0.0001$; ***$p < 0.001$; **$p < 0.01$; *$p \leq 0.05$.

(a) Species present only in one FD scenario

(b) Species present in two FD scenarios

* Symbol † next to the species name indicates significant differences between low and high initiall functional diversity scenarios: see statistical analyses in Appendix III.

(a) Species present only in one FD scenario

(b) Species present in two FD scenarios

* Symbol † next to the species name indicates significant differences between low and high initiall functional diversity scenarios: see statistical analyses in Appendix V.

FIGURE 4 Mean number of fruits per fruiting plant in species with significant differences between treatments/scenarios (see Table 2 for the statistical models for all species). (a) Species present only in one initial functional diversity scenario (mixed, or small-, or large-sized species). (b) Species present in two initial functional diversity scenarios (mixed and small, or mixed and large-sized species). Vertical bars represent standard errors. We conducted post hoc Tukey's tests for differences between biological soil crust (BSC) treatments for each species. Horizontal bars above the mean values indicate pairs of cases responsible for significant differences and asterisks the level of significance: ****$p < 0.0001$; ***$p < 0.001$; **$p < 0.01$; *$p \leq 0.05$.

diversity denoting that species with different maximum statures may most likely avoid competition among them resulting in larger investment in fruit production of plants in highly diverse scenarios.

Intact lichen portions of BSC substantially reduced the plant abundance of many species independently of the FD scenarios. Luzuriaga et al. (2015) showed that the lichen-dominated BSC in these gypsum outcrops tend to reduce the richness, diversity and total cover of annual plant assemblages. Indeed, much evidence supports the restrictive effects of BSC-forming lichens on seedling emergence (Deines et al., 2007; Escudero et al., 2007; Ghiloufi & Chaieb, 2016; Havrilla et al., 2019; Hawkes & Menges, 2003; Serpe et al., 2008; Zamfir, 2000). In particular, Deines et al. (2007) and Serpe et al. (2008) showed that BSC dominated by *Diploschistes muscorum* (Scop.) R. Sant. formed a physical barrier that dramatically reduced seed hydration and germination, radicle rooting and seedling establishment by annual species. Similar effects of *D. diacapsis* on the tussock perennial grass *Macrochloa tenacissima* (L.) Kunth were reported by Ghiloufi and Chaieb (2016), but not by the squamulose lichen *Fulgensia bracteata* (Hoffm.) Räsänen, thereby highlighting the strong species-specific interactions between vascular plants and BSC (Maestre et al., 2011; Zhang et al., 2016). Within this species-specific interaction framework, Escudero et al. (2007) found that both of the lichens in our experimental BSC material, *D. diacapsis* and *S. lentigera*, reduced seedling emergence by gypsophile plant species despite the ability of these plant specialists to penetrate extremely hard physical crusts (Meyer, 1986; Romão & Escudero, 2005). The two lichens differ in terms of their thallus morphology (i.e. crustose and foliose, respectively; Eldridge & Rosentreter, 1999) but both adhere firmly to the substrate to form a very hard crust, which might not be easily penetrated by the roots emerging from the radicles of germinating seeds, thereby imposing a severe physical constraint (Romão & Escudero, 2005). In addition, many lichens found in BSC can produce chemical compounds that affect the germination success of some plant species (Deines et al., 2007; Escudero et al., 2007; Zhang et al., 2016). However, Escudero et al. (2007) did not obtain conclusive evidence for this effect of our experimental lichen species, and Deines et al. (2007) excluded allelopathic effects of *Diploschistes*. In contrast to the restrictive effect of the intact BSC, the plant abundances in our assemblages were affected little by the disaggregated BSC treatment compared with bare soil (i.e. only a slight reduction under the large-sized species scenario, which generally decreased plant establishment), and thus our results support the idea that although the allelopathic properties of the BSC cannot be disregarded, physical restriction was more important than any other effects when the soil adhered firmly to the lichens with a relatively large thallus.

Despite this restrictive BSC effect, we did not detect any consistent plant-establishment response pattern mediated by FD of the MPH of species, beyond some cases (four experimental species), which established more abundant in highly than in low diverse scenarios, and a non-BSC-dependent lower plant abundance in some large-sized species (e.g. *Eruca vesicaria*, *Stoibrax dichotomum*,

Limonium echioides). The former may be the consequence of niche complementarity (Chaves et al., 2021) attenuating some kind of competition which in fact became much more evident in last phases of the life cycle, when the intensity of competitive interactions should made particularly high. The latter, opposed to Peralta et al. (2019) results, may be linked to the often-recorded correlation between plant height and seed mass (Garnier et al., 2016; Moles & Leishman, 2008). Indeed, seeds of the species in our large-sized plant combinations were larger than those of the small species (2.36 vs. 0.65 mg on average). A plausible explanation for the lower success of plant establishment in those large-sized species may be the greater difficulty of their seeds entering the soil when in contact with the substrate particles due to their larger dimensions, especially when intact portions of the compact lichen dominated (e.g. Briggs & Morgan, 2011). Seed size and the morphology of BSC components are related to germination because the combination of both features greatly determines the availability of suitable microsites (Escudero et al., 2007; Li et al., 2005; Zamfir, 2000). Based on manipulative experiments with the entire annual plant community and the natural BSC in these gypsum systems, Peralta et al. (2019) found that the BSC tended to prevent seedling establishment by large seeded species. Furthermore, when BSC were disaggregated under water scarce conditions, they detected a filtering effect of BSC on plant height (and other traits related to plant economics) to favour short species during annual plant assemblage formation. However, water was not limiting in our experiment (see Appendix S1). Luzuriaga et al. (2012) found no filtering effect of BSC on annual plant assemblages in gypsum outcrops during wet years. Overall, our results suggest that one of the main net effects of the lichen-dominated BSC was as a locally widespread hard barrier against plant establishment, thereby significantly affecting fine scale soil heterogeneity (Concostrina-Zubiri et al., 2013) the assembly of annual plants in these systems. In addition, this effect of BSC will determine the assembly process because the early phases of the life cycle are crucial for determining the annual plant community features throughout the whole growing season (Donohue et al., 2010; Jiménez-Alfaro et al., 2016; Luzuriaga et al., 2012; Peralta et al., 2019).

In contrast to the restrictive effect during the establishment of the assemblages, the intact and disaggregated forms of the BSC favoured vegetative growth and fitness (i.e. number of fruits per plant) for most plant species in pots. This type of shifting BSC interaction throughout the life cycle of annual plants has been documented previously in these systems (Peralta et al., 2019) and it illustrates the complexity of the relationships between both groups of organisms (Maestre et al., 2011; Zhang et al., 2016). BSC can significantly ameliorate the harsh soil conditions in drylands by increasing soil water infiltration and reducing evaporation (Berdugo et al., 2014; Chamizo et al., 2012; Maestre et al., 2002), as well as by actively participating in nutrient cycling (Bowker et al., 2010; Cline & Rickard, 1973), fixation of atmospheric nitrogen (Cortina et al., 2010; Harper & Belnap, 2001), and the retention of sediments and organic matter (DeFalco et al., 2001; West, 1990). In this study, water stress was not an issue due to the humidity in the greenhouse and pot watering

conditions. However, nutrients may have been limiting in the bare soil treatment because it comprised seed-free gypsum soil from a quarry with an extremely infertile substratum, and imbalanced nutrients (Escudero et al., 2015; Gankin & Major, 1964; Meyer, 1986) with no significant sources of organic matter. In several, probably joint ways, BSC should be acting as a crucial fertilizing biotic layer for plant life in these restrictive environments.

FDThe effects of initial FD of assemblages on plant performance of experimental species were particularly insightful about mechanisms operating in the assembly process. When analysing the response of species present in two MPH assemblage scenarios, we found that plants in low FD scenarios (i.e. large or small sized) prioritized allocation to growth (Figure 3b) over reproduction (Figure 4b), while the opposite was observed in high FD (i.e. mixed sized) scenarios. Plant stature has been related to the competitive capacity for light interception, and thus it is an essential feature of the carbon acquisition strategies of plants (Garnier et al., 2016; King, 1990; Westoby et al., 2002). Similar to other annual species in desert systems (Ben-Hur & Kadmon, 2015), competitive relationships may have been crucial for organizing our model plant community, mainly because these communities comprise ephemeral herbaceous species with closely synchronized life cycles (Luzuriaga et al., 2012) that form dense assemblages (Escudero et al., 2015; Luzuriaga et al., 2012). Equalizing symmetric competition among species may be a pivotal mechanism operating on the organization of our low FD assemblages. Here, plants with similar competitive ability defined by the MPH may be driven to invest more resources in growth, as an attempt to surpass or equalize the stature of interacting neighbours within their species plasticity range. In mixed plant sized scenarios, that is, high FD assemblages, plants were not advocated to intensely compete in growth: the mitigation of competition by differences in stature, which in addition may favour a more efficient both above- and below-ground space filling (Pacala & Levin, 1997), should allow plants to better share resources by niche partitioning and thus a higher investment in the fruit production, resulting in a high fitness of interacting species. From a phylogenetic perspective, Chaves et al. (2021) suggested diversity in assemblages as a plausible selection force in the evolutionary processes of species in these communities.

The results obtained in this study highlight the complex relationships between two conspicuous biological components of drylands around the world. BSC greatly determine the assembly of annual plants via various effects with opposing outcomes on plant performance. Our experiment showed that the restrictive hard barrier imposed by the lichen-dominated BSC on the early plant establishment phase in drylands may comprise a strong environmental determinant for plant assembly at a heterogeneous fine spatial scale (Concostrina-Zubiri et al., 2013). Contrastingly, in late life stages, BSC-forming lichens may ameliorate the harsh microclimatic conditions for plants, which could be crucial for plant communities that live in stressful systems and with strong organization via competitive relationships. Indeed, our results highlight niche segregation as

an effective mechanism promoting species fitness in these annual gypsum plant communities, as proposed by Chaves et al. (2021) who showed that niche complementarity may mitigate the competitive intensity among neighbouring plants as a major assembly mechanism to promote phylogenetically diverse assemblages in nature. Importantly, we found that the FD structure of the community relative to the maximum plant size could also determine assembly mechanisms, which may activate alternative coexistence modes such as niche partitioning or competition symmetry depending on plant neighbourhood features. This effect was irrespective of BSC conditions, stressing the importance of plant neighbourhood features on the community organization. Moreover, the barrier effect of the BSC may substantially contribute to determine the initial FD of the assemblage in natural conditions, thereby activating species coexistence mechanisms to affect the fitness of the species in the community.

AUTHOR CONTRIBUTIONS

Arantzazu L. Luzuriaga conceived the idea, performed the experimental design and outlined the statistical analyses; Arantzazu L. Luzuriaga and Pablo Ferrandis designed the methodology; Arantzazu L. Luzuriaga, Pablo Ferrandis and Laura Ortiz collected the seeds for the experimental setup; Laura Ortiz collected and analysed the data; Laura Ortiz and Pablo Ferrandis led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.6hdr7sr4p.

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