María Laura Ortiz Díaz
Species assembly and coexistence mediated by phylogenetic and functional diversities: an experimental perspective in plant communities of semiarid gypsum systems
Universidad Rey Juan Carlos

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TESIS DOCTORAL

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Entender los procesos de ensamblaje y de coexistencia de especies que forman una comunidad ha sido, y sigue siendo, uno de los principales objetivos de la ecología de comunidades. Las diferentes teorías y enfoques que tratan de explicar estos procesos han ido evolucionando a lo largos de los años. Así, desde un primer enfoque en el que se consideraba que solo ciertas combinaciones de especies podían ocurrir en la naturaleza, el abanico se amplía hasta la idea de que las comunidades son simplemente una coincidencia de especies modulada por el azar, en el que tanto procesos de llegada de propágulos al sistema como de deriva ecológica adquieren gran protagonismo. Todos estos enfoques han generado interesantes debates a lo largo del tiempo, siendo el más reciente el que enfrenta los postulados de las Teorías de Nicho (Hutchinson, 1957) y Teoría de la Neutralidad (Hubbell, 2001), si bien la comunidad científica, conforme avanza en el estudio de ambas, se aproxima a una integración de procesos estocásticos y deterministas, pues asume que los dos tipos participarían decisivamente en la conformación de las comunidades. Cómo apuntábamos, ambos enfoques han recibido mucha atención, pero la mayoría de los estudios se han basado principalmente en diseños observacionales, debido a la dificultad de manipular comunidades enteras.

Sin embargo, para seguir avanzando en el conocimiento de las reglas de ensamblaje y de los mecanismos de coexistencia implicados en la formación de la comunidad, urge un planteamiento experimental, factible mediante la manipulación de las propiedades funcionales y filogenéticas de la comunidad, en combinación con la de los factores abióticos y bióticos que operan durante el proceso de ensamblaje, para establecer inequívocamente relaciones causa-efecto. Además, actualmente, se han refinado mucho las herramientas fundamentales con las que contamos para estudiar la comunidad desde un enfoque no solo taxonómico, sino funcional y filogenético. La diversidad funcional nos aporta información sobre los efectos de filtrado de los factores ambientales sobre las características funcionales de los organismos en un sistema, mientras que la diversidad filogenética resume las características morfológicas, fisiológicas, metabólicas y fenológicas a lo largo de la evolución de las especies. Con esta Tesis Doctoral nos proponemos explorar los mecanismos de ensamblaje y coexistencia

de especies en el contexto de las Teorías de Nicho y Teorías de la Neutralidad de neutralidad a través de una aproximación experimental, manipulando la diversidad funcional y filogenética de partida de ensambles completos, mediante experimentos de jardín común en invernadero con plantas anuales, así como los filtros ambientales que operan sobre los ensambles naturales, mediante experimentos de campo.

Objetivos

El objetivo principal de esta tesis doctoral es tratar de definir los principales mecanismos de ensamblaje y coexistencia de especies que predominan en nuestra comunidad vegetal modelo, aquella dominada por plantas anuales que vive en estepas yesosas del centro de la Península Ibérica, desde una aproximación experimental. Para ello, trataremos de (1) definir tanto la contribución relativa de los procesos estocásticos, representados en nuestro estudio por la llegada de propágulos, como la de los procesos deterministas, representados por el filtrado ambiental biótico y abiótico, en la formación local de nuestras comunidades vegetales; y (2) analizar en qué medida las propiedades funcionales y filogenéticas del propio ensamble, esto es, las características ecológicas y evolutivas de las plantas vecinas, afectan al rendimiento de las especies coexistentes. Como aproximación a la evaluación de la importancia de los procesos estocásticos, analizaremos hasta qué punto la disponibilidad de semillas en el suelo influye en los procesos de ensamblaje de plantas en estos sistemas semiáridos, y como aproximación al filtrado ambiental, analizaremos cómo estas respuestas pueden estar afectadas por la presencia de esparto (*Macrochloa tenacissima*) y por la costra biológica del suelo (CBS) (elementos bióticos ampliamente representados en nuestra comunidad), o por la variabilidad interanual de la disponibilidad hídrica. Estudiaremos, además, hasta qué punto las partes aérea y subterránea de las macollas vivaces de *M. tenacissima* pueden afectar diferencialmente a la conformación de las comunidades vegetales en las estepas yesosas y si el riego, y por lo tanto la relajación del filtro abiótico, puede modular dichos efectos bióticos sobre los procesos de ensamblaje. Por otro lado, trataremos de determinar si la respuesta de las especies anuales al filtrado de la CBS está modulada por la propia diversidad funcional de los ensambles de los que forman parte, definida en este caso por la altura máxima de la planta (MPH). Además, manipularemos las diversidades filogenéticas y funcionales iniciales en comunidades completas, con el fin de estudiar los efectos independientes e interactivos de la estructura tanto filogenética como funcional de los ensambles experimentales sobre el desarrollo y fitness de las plantas participantes. Todo ello, con el fin de definir inequívocamente relaciones causa-efecto que nos permitan identificar los principales procesos de ensamblaje y de coexistencia de especies.

Metodología

Hemos centrado nuestro estudio en las comunidades vegetales dominadas por plantas anuales en un sistema yesífero del tramo medio del valle del Tajo, entre Madrid y la Mesa de Ocaña, en el centro de la Península Ibérica. El clima dominante en este sistema es mediterráneo semiárido, caracterizado por la gran variabilidad en la cantidad y el momento de las precipitaciones entre años. La estructura de la comunidad vegetal está formada por parches de plantas intercalados dentro de una matriz de suelo desnudo con abundante presencia de costra biológica del suelo (CBS), bien desarrollada. La vegetación aérea está dominada principalmente por macollas de la gramínea perenne *Macrochloa tenaccisima* y algunos arbustos camefíticos especialistas gipsófilos, entre los que prolifera estacionalmente una rica y dinámica comunidad de plantas anuales a partir de un amplio pool regional de especies. En estos ambientes, los ensambles se organizan bajo filtrados ambientales, abióticos y bióticos, de intensidad muy variable en el espacio y en el tiempo, lo que propicia la evaluación de reglas de ensamblaje. Además, algunas de las características generales del pool regional de especies anuales ofrecen posibilidades excepcionales de experimentación a partir de diseños manipulativos sobre comunidades completas, al tratarse de plantas de pequeño tamaño, lo que permite el montaje de ensambles experimentales completos en espacios reducidos y manejables (i.e., macetas), con ciclos de vida sincronizados y cortos, por lo que se pueden obtener resultados concluyentes en periodos relativamente breves de tiempo, libres además de los efectos cambiantes derivados de la ontogenia.

Para alcanzar los objetivos propuestos en este estudio, hemos realizado cuatro experimentos manipulativos: dos experimentos de campo y dos experimentos de jardín común en invernadero. Los dos experimentos de campo se realizaron en la Estación de Campo Experimental de Sotomayor, situada en Aranjuez, centro de España, (40°01′55.7″N - 3°32′48.3″W, 590 m). Esta localización presenta las condiciones mediterráneas semiáridas descritas anteriormente y una buena representación de nuestras comunidades vegetales modelo. Con los experimentos de campo intentamos estudiar el papel de la llegada de semillas al sistema (proceso estocástico), la contribución de los principales filtros bióticos (presencia de plantas perennes y costra biológica del suelo), así como el papel de la disponibilidad de agua, el filtro abiótico más relevante en nuestro sistema. Los experimentos en invernadero se han desarrollado mediante la técnica del "jardín común" con las plantas anuales gipsófilas de nuestro sistema. Esta técnica nos permite recrear comunidades en macetas y replicarlas, controlando las propiedades funcionales y filogenéticas de partida en los ensambles y aplicar tratamientos de filtrado abiótico y biótico bajo condiciones controladas. Con estos experimentos tratamos de explorar el efecto causal de la diversidad funcional y filogenética inicial de nuestras comunidades sobre el rendimiento de las plantas participantes en los ensambles, con el fin de definir los mecanismos de ensamblaje y de coexistencia de especies.

Resultados

En el capítulo 1, basado en un experimento de campo manipulativo de disponibilidad de semillas en el suelo y la presencia de diferentes factores ambientales (macollas vivaces de *M. tenacissima*, CBS, áreas abiertas), con seguimiento durante 4 años consecutivos, nuestros resultados demostraron que, en años con precipitaciones iguales o superiores a la media, los procesos estocásticos dominaron sobre los deterministas en los procesos de ensamblaje de especies. Aunque los factores ambientales afectaron a la cobertura total de plantas y a la diversidad taxonómica, no generaron una selección de especies basada en sus rasgos funcionales. Además, cabe destacar el papel desempeñado por la presencia de CBS, ya que su presencia aumentó ostensiblemente la riqueza, la cobertura total y la diversidad taxonómica incluso en condiciones iniciales de suelo libre de semillas.

En el capítulo 2, basado en un experimento de campo manipulativo de las macollas vivaces de *M. tenacissima*, la disponibilidad de semillas en el suelo y la abundancia hídrica, nuestros resultados mostraron un efecto generalmente negativo de las macollas de *M. tenacissima* sobre las comunidades de plantas anuales. La parte subterránea, es decir la parte radicular de *M. tenacissima* tuvo un efecto negativo sobre las comunidades de plantas anuales, reduciendo tanto la riqueza como la cobertura vegetal, probablemente relacionado con la competencia subterránea por los recursos. También podemos concluir que no hubo una clara selección de rasgos funcionales por la presencia de *M. tenacissima* (o cualquiera de sus partes). Nuestros resultados volvieron a confirmar la importancia de la disponibilidad de semillas en nuestros sistemas; además, demostramos que los suelos libres de semillas necesitaron más tiempo del esperado para igualarse con los suelos que presentaban bancos de semilla naturales completos, lo que jugó un papel importante en la riqueza de especies, cobertura vegetal y selección de rasgos en nuestro sistema de yeso dominado por anuales.

En el capítulo 3, basado en la creación experimental de ensambles de plantas anuales con valores contrastados de diversidad funcional (basada en el rasgo altura máxima de la planta-MPH-) predeterminada y bajo diferentes condiciones de CBS, nuestros resultados mostraron que la presencia de CBS afectó al establecimiento y desarrollo de plantas anuales gipsófilas de una manera compleja y diferente a lo largo del ciclo de vida de la planta. La CBS, dominada por líquenes, actuó como una primera barrera física afectando al establecimiento de las plantas anuales. Este efecto restrictivo fue particularmente marcado cuando la CBS se encontraba intacta, sin perturbaciones. Sin embargo, para las plantas anuales que superaron esa primera restricción impuesta por la CBS, la misma capa biótica facilitó el crecimiento y fitness de las plantas, dando lugar a plantas más grandes que produjeron más frutos. La diversidad funcional inicial de los ensambles creados en este experimento influyó en los mecanismos de ensamblaje de estos. En escenarios con alta diversidad funcional predominó la complementariedad de nicho, mientras que en escenarios con baja diversidad funcional (escenarios con presencia de plantas solo pequeñas o solo grandes) las especies invirtieron más recursos en crecer y competir en altura que en la reproducción.

En el capítulo 4, basado en la creación de numerosas combinaciones de especies generando un gradiente de diversidad filogenética en ensambles experimentales, en los que se midió posteriormente la diversidad funcional de tres rasgos fundamentales en la definición de las estrategias ecológicas de las plantas (estatura vegetativa de la planta, MPH; área específica de la hoja, SLA; peso de la semilla, SM), nuestros resultados mostraron que en los escenarios que presentaban una disponibilidad de agua equivalente a la media histórica para nuestro sistema, es decir, sin estrés hídrico, la mayoría de las especies de plantas anuales pudieron completar con éxito sus ciclos vitales (más del 75% de los individuos de cada especie produjeron frutos), independientemente de las diversidades filogenéticas y funcionales iniciales. En los vecindarios filogenéticamente más diversos, sin embargo, las plantas completaron sus ciclos vitales en un lapso de tiempo más corto que en los menos diversos. Además, cuando redujimos la disponibilidad de agua, las especies que crecían en vecindarios filogenéticamente más diversos presentaron una mayor proporción de plantas que llegaban a fructificar que aquellas que crecían en vecindarios compuestos por parientes más cercanos. Asimismo, bajo sequía, las especies produjeron mayor cosecha de semillas en escenarios de mayor diversidad filogenética. La diversidad funcional de los rasgos MPH, SLA y SM, así como la de un índice multifuncional formado por la combinación de los tres rasgos, produjeron una interacción significativa entre las diversidades filogenética y funcional iniciales sobre la supervivencia y fructificación de las especies que coexistían: en estos condiciones de estrés hídrico, la proporción de plantas fructíferas por especie aumentó con la diversidad funcional hasta un cierto umbral, donde disminuyó formando una tendencia unimodal.

Conclusiones

Con este trabajo hemos dado un paso sustancial en la comprensión de cómo se forma una comunidad y cómo conviven las especies que se encuentran en ella en condiciones ambientales adversas. Concretamente, el enfoque innovador que presentamos en esta tesis, basado en la manipulación experimental de las propiedades de los ensambles y/o de los filtros ambientales operando sobre los procesos de configuración de la comunidad, ha permitido evaluar empíricamente hipótesis inaccesibles desde el enfoque observacional clásico y aportar nueva información sobre las reglas de ensamblaje que actúan en los sistemas yesíferos del centro de la Península Ibérica.

Nuestros resultados demuestran que, en los sistemas semiáridos de yesos, la estocasticidad podría ser el principal impulsor de los procesos de ensamblaje, durante años con precipitaciones igual o superiores a la media. En estas condiciones, los procesos estocásticos predominaron frente a los procesos deterministas en el ensamblaje de nuestra comunidad. Corroboramos que la disponibilidad hídrica marcada por la alta variabilidad climática interanual intervendría como un primer filtro de especies que forman el pool regional de especies de nuestro sistema. Confirmamos además la importancia de la disponibilidad de semillas en el suelo y de los microambientes creados por los componentes bióticos (presencia de *Macrochloa tenacissima* y costra biológica del suelo -CBS- en este caso), que influyeron decisivamente en la formación de las comunidades de plantas. La presencia de *M. tenacissima* no tiene un claro efecto facilitador. Además, su porción subterránea radicular parece competir predominantemente por los recursos. En cuanto a la presencia de CBS, actúa en un primer momento como filtro físico dificultando la entrada de algunas especies, pero las que consiguen establecerse se benefician de la mejora de las condiciones por parte de la CBS, traduciéndose en un mayor crecimiento y fitness de las plantas.

Nuestros resultados también apuntan a que las comunidades de plantas anuales en sistemas yesíferos semiáridos ibéricos parecen estar fuertemente organizadas en torno a relaciones competitivas, lo que haría de la complementariedad de nicho uno de los mecanismos centrales de ensamblaje bajo condiciones de estrés hídrico. Notablemente, la diversidad funcional inicial de las comunidades determinaría mecanismos de coexistencia alternativos, como la partición de nicho o la simetría competitiva, dependiendo de las características de las plantas vecinas, lo que subraya la implicación de las propiedades funcionales del ensamble en la determinación de los mecanismos de coexistencia de especies en torno a los cuales se organiza la comunidad, más allá de los procesos de filtrado ambiental clásicamente contemplados en la ecología de comunidades. Además, una mayor diversidad filogenética en los ensambles favorecería el éxito de las plantas ya que, las especies más alejadas son menos parecidas en términos del uso de recursos y, por tanto, presentarían mayor complementariedad de nichos. Tanto la diversidad funcional como la diversidad filogenética aportarían información complementaria para comprender los mecanismos de coexistencia de las especies. Mientras que la diversidad filogenética integra toda la historia evolutiva de las especies, la variabilidad adicional que explica la diversidad funcional, está probablemente relacionada con cambios evolutivos más recientes.

SUMMARY

Background

Understanding the assembly process and species coexistence forming a community are still one of the main objectives of community ecology. The different theories and approaches trying to explain these processes have evolved over the years. From an early approach in which it was considered that only certain combinations of species could occur in nature, to the idea that communities are simply a coincidence of species, where arrival of propagules and ecological drift play a major role. All these approaches have generated interesting debates over time, reaching the most recent one between Niche Theory and Neutrality Theory. Nowadays, the scientific community is moving towards an integration of both processes (stochastic and deterministic), understanding that both play a decisive role in the formation of communities. Although both approaches have received much attention, most studies have based mainly on observational studies due to the difficulty of manipulating whole communities.

However, further progress in understanding the assembly rules and coexistence mechanisms involved in community formation requires an experimental approach, feasible by manipulating the functional and phylogenetic properties of the community, in combination with the abiotic and biotic factors operating during the assembly process, to unequivocally establish cause-effect relationships. Moreover, the fundamental tools available to study the community not only taxonomically, but also functionally and phylogenetically, have now been greatly refined. Functional diversity provides information on the filtering effects of environmental factors present in a system, while phylogenetic diversity summarises morphological, physiological and phenological characteristics throughout the evolution of species. Therefore, with this thesis we aim to explore the mechanisms of species assemblage and coexistence in the context of niche and neutrality theories through an experimental approach, manipulating the functional and phylogenetic diversity of complete assemblages via common garden experiments in greenhouses with annual plants, as well as the environmental filters operating on natural assemblages via field experiments.

Objectives

The main objective of this thesis is to try to define the main assembly mechanisms of species and coexistence that predominate in our model plant community, dominated by annual plants living in gypsum steppes in the centre of the Iberian Peninsula, from an experimental approach. To this end, we will try to (1) define both the relative contribution of stochastic processes, represented in our study by the arrival of propagules, and deterministic processes, represented by biotic and abiotic environmental filtering, to the local formation of our plant communities; and (2) analyse to what extent the functional and phylogenetic properties of the assemblage itself, i.e. the ecological and evolutionary characteristics of neighbouring plants, affect the performance of coexisting species. As an approach to assess the importance of stochastic processes, we will analyse how the availability of seeds in the soil influences plant assemblage processes in these semiarid systems, and as an approach to environmental filtering, we will analyse how these responses may be affected by the presence of tussock grass (*Macrochloa tenacissima*) and biological soil crust (BSC) (biotic elements widely represented in our community), or by the interannual variability of water availability. We will also study to what extent the aboveground and belowground parts of the perennial plants of *M. tenacissima* can differentially affect the conformation of plant communities in gypsiferous steppes and whether irrigation, and therefore the relaxation of the abiotic filter, can modulate these biotic effects on the assemblage processes. On the other hand, we will try to determine whether the response of annual species to BSC filtering is modulated by the initial functional diversity of the assemblages, defined in this case by maximum plant height (MPH). In addition, we will manipulate the initial phylogenetic and functional diversities in complete communities, in order to study the independent and interactive effects of both the phylogenetic and functional structure of the experimental assemblages on the development and fitness of the participating plants. All this, in order to unequivocally define cause-effect relationships that allow us to identify the main processes of assemblage and coexistence of species.

Methodology

We have focused our study on the plant communities dominated by annual plants in a gypsiferous system in the middle section of the Tagus valley, between Madrid and Mesa de Ocaña, in the centre of the Iberian Peninsula. The climate dominated in this system is semiarid Mediterranean characterized by the highly variable amount and timing of precipitation among years. The plant community structure is formed by plant patches within a matrix of bare soil and abundant well-developed biological soil crusts (BSC). The aboveground vegetation is mainly dominated by perennial tussock grasses of *Macrochloa tenaccisima* and some specialist gypsophilous cameophytic shrubs, interspersed proliferates a rich and dynamic annual plant community seasonally from a broad regional pool of species. In these environments, the assemblages are organised under environmental, abiotic and biotic filters, of highly variable intensity in space and time, which facilitates the evaluation of assembly rules. In addition, some of the general characteristics of the regional pool of annual species offer exceptional possibilities for experimental manipulation of complete communities: they are small plants, which allows the assembly of complete experimental assemblages in reduced and manageable spaces (i.e., pots), with synchronised and short life cycles, allowing conclusive results in short periods of time, free of the changing effects derived from ontogeny.

To achieve the objectives proposed in this study, we have performed four manipulative experiments: two field experiments and two common garden experiments in a greenhouse. The two field experiments were conducted at the Sotomayor Experimental Field Station, located in Aranjuez, central Spain, (40°01′55.7″N - 3°32′48.3″W, 590 m). This location presents the semiarid Mediterranean characteristics described above and a well representation of our model plant communities. With the field experiments we tried to study the role of seed arrival in the system (stochastic process), the contribution of the main biotic filters (presence of perennial plants and biological soil crust), as well as the role of water availability, the most relevant abiotic filter in our system. The greenhouse experiments have been developed using the "common garden" technique with the annual gypsophilous plants of our system. This technique allows us to recreate communities in pots and replicate them, controlling the initial functional and phylogenetic structures of the assemblages and applying abiotic and biotic filtering treatments under controlled conditions. With these experiments we try to explore the causal effect of the initial functional and phylogenetic diversity of our communities on the performance of the plants participating in the assemblages, in order to define the assembly mechanisms and coexistence of species.

Results

In chapter 1, based on a manipulative field experiment on soil seed availability and the presence of different biotic filters (perennial plants of *M. tenacissima*, BSC, open areas), monitored for 4 years, our results showed that, in years with average or above rainfall, stochastic processes dominated over deterministic processes in species assemblage processes. Although environmental factors affected total plant cover and taxonomic diversity, they did not generate a selection of species based on their functional traits. Furthermore, the role played by the presence of BSC is noteworthy, as its presence significantly increased richness, total cover and taxonomic diversity even under initial seed free soil conditions.

In chapter 2, based on a manipulative field experiment of *M. tenacissima* perennial plants, soil seed availability and water abundance, our results showed a generally negative effect of *M. tenacissima* on annual plant communities. The underground part, i.e. the root part of *M. tenacissima* had a negative effect on annual plant communities, reducing richness and plant cover, probably related to belowground competition for resources. We can also conclude that there was no clear selection for functional traits by the presence of *M. tenacissima* (or any of its parts). Our results reconfirmed the importance of seed availability in our systems; furthermore, we showed that seed free soils took longer than expected to recover and equalise with soils with intact natural seed banks, which played an important role in species richness, plant cover and trait selection in our annual-dominated gypsum system.

In chapter 3, based on the experimental creation of annual plant assemblages with predetermined functional diversity (based on the MPH trait) and under different BSC conditions, our results showed that the presence of BSC affected the establishment and development of gypsophilous annual plants in a complex and different way throughout the plant life cycle. The lichen-dominated BSC acted as a first physical barrier affecting the establishment of annual plants. This restrictive effect was particularly marked when the BSC was intact, undisturbed. However, for annual plants that overcame this first restriction imposed by the BSC, the same biotic layer facilitated plant growth and fitness, resulting in larger plants that produced more fruit. The initial functional diversity of the assemblages created in this experiment influenced their assembly mechanisms. In scenarios with high functional diversity, niche complementarity predominated, whereas in scenarios with low functional diversity (scenarios with only small or large plants), species invested more resources in growth and height competition than in reproduction.

In chapter 4, based on the creation of numerous species combinations generating a gradient of phylogenetic diversity in experimental assemblages, in which the functional diversity of three fundamental traits in the definition of plant ecological strategies (plant vegetative stature, MPH; specific leaf area, SLA; seed weight, SM) was subsequently measured, our results showed that in scenarios where we provided water availability equivalent to the historical average for our system, i.e. no water stress, most annual plant species were able to successfully complete their life cycles (more than 75% of individuals of each species produced fruit), regardless of initial phylogenetic and functional diversities. In phylogenetically more diverse neighbourhoods, plants completed their life cycles in a shorter time span than in less diverse ones, and when we reduced water availability, species growing in phylogenetically diverse neighbourhoods had a higher proportion of plants that reached fruiting than those growing in neighbourhoods composed of closer relatives. Moreover, fruiting species also produced more seeds in assemblages phylogenetically more diverse. Functional diversity, in this case, of MPH, SLA and SM traits, as well as a multi-trait index, there was a significant interaction between the initial phylogenetic and functional diversities on the proportion of plant survival and fruiting plants, in these cases, the proportion of fruiting plants per species increased with functional diversity up to a certain threshold, where it decreased forming a unimodal trend.

Conclusions

With this work we have taken a substantial step forward in the understanding of how a community is formed and how the species found in it coexist under adverse environmental conditions. Specifically, the innovative approach presented in this thesis, based on the experimental manipulation of assembalge properties and/or environmental filters operating on assemblage processes, has allowed us to empirically evaluate hypotheses inaccessible from the classical observational approach and to provide new information on the assembly rules acting in the gypsiferous systems of the central Iberian Peninsula.

Our results show that in semiarid gypsum systems, stochasticity could be the main driver of assembly processes. During years with average or above-average rainfall, stochastic processes dominated over deterministic processes in the assemblage of our community. We corroborate that water availability, marked by high interannual climatic variability, would act as t first filter of species that form the regional species pool in our system. We also confirmed the importance of the availability of seeds in the soil and the microenvironments created by biotic components (presence of *Macrochloa tenacissima* and biological soil crust -BSC- in this case), which influenced the formation of plant communities. The presence of *M. tenacissima* does not have a clear facilitating effect, moreover, its belowground part (root system) seems to compete for resources. On the other hand, the presence of BSC acts initially as a physical filter, affecting the establishment of some species, but those that manage to establish benefit from the improved conditions provided by the BSC, resulting in increased growth and plant fitness.

This study confirms that annual plant communities in Iberian semi-arid gypsiferous systems seem to be strongly organised around competitive relationships, which would make niche complementarity one of the central assembly mechanisms under water stress conditions. Notably, the initial functional diversity of the communities would determine alternative coexistence mechanisms, such as niche partitioning or competitive symmetry, depending on the characteristics of neighbouring plants, underlining the implication of the functional properties of the assemblage in determining the mechanisms of species coexistence forming the community, beyond the environmental filtering processes classically contemplated in community ecology. In addition, greater phylogenetic diversity in assemblages would favour plant success, if we assume that as more distant species are less similar in terms of resource use and therefore present more complementary niches. Both functional diversity and phylogenetic diversity would provide complementary information for understanding the mechanisms of species coexistence. While phylogenetic diversity probably integrates the entire evolutionary history of species, the additional variability that explains functional diversity is probably related to more recent evolutionary changes.

INTRODUCCIÓN GENERAL

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La comunidad científica ha hecho un gran esfuerzo por comprender y clasificar los procesos que intervienen en la formación y establecimiento de una comunidad (Keddy & Laughlin, 2021). La ecología de comunidades ha centrado estos esfuerzos en investigar la naturaleza de las interacciones entre organismos, sus orígenes y sus consecuencias tanto ecológicas como evolutivas (Vellend, 2010; Cavender-Bares et al., 2009). Para ello ha intentado comprender los procesos que generan variaciones en la diversidad, identidad y abundancia de las especies que coexisten (Kraft et al., 2007), es decir, en los procesos de ensamblaje y de coexistencia de las especies que forman una comunidad. Son muchas las preguntas que plantean estos procesos y que durante mucho tiempo se han intentado contestar mediante diferentes teorías. Dos de estas teorías son precisamente las que han generado un gradiente conceptual en el cual enfocaremos este estudio. Este gradiente conceptual va desde la teoría determinista propuesta por Clements (1916) a la teoría estocástica, propuesta por Gleason (1926). Esta dicotomía de teorías continuó con las publicaciones de Diamond (1975) y la posterior respuesta de Connor & Simberloff (1979), también con el más reciente debate entre la teoría de nicho (Chase & Leibold, 2003) frente a la teoría de la neutralidad (Rosindell et al., 2011; Hubbell, 2001). A esta serie de teorías se les han unido diferentes trabajos que también intentan abordar el conocimiento del ensamblaje de comunidades (Escudero & Valladares, 2016; Götzenberger et al., 2012; HilleRisLambers et al., 2012; Myers & Harms, 2011; Chase & Myers, 2011; Vellend, 2010; Weiher et al., 2011; Lortie et al., 2004; Zobel et al., 2000) (Figure 1).

Procesos deterministas *vs.* estocásticos

En un primer enfoque, los procesos deterministas (Clements, 1916) sugieren que en la naturaleza solo pueden darse determinadas combinaciones de especies, de tal modo y, según la Teoría del Nicho (Hutchinson, 1957) las comunidades se organizarían atendiendo a una serie de reglas de ensamblaje definidas. Las interacciones de facilitación y/o competencia entre especies, el nicho ecológico y la heterogeneidad ambiental tendrían un papel crucial en la creación de la comunidad (Chase & Myers, 2011). Por otro lado, los procesos estocásticos sugieren que la comunidad es simplemente una coincidencia de especies y otorga una gran importancia a la llegada de propágulos al sistema (Myers & Harms, 2011; Zobel et al., 2000), la Teoría de la Neutralidad aboga además por la equivalencia de la eficacia biológica de las especies (Hubbell, 2001). Con nuestra comprensión actual hemos llegado a un consenso generalizado que asume que tanto los procesos deterministas como los estocásticos operan conjuntamente y desempeñan una función decisiva en la formación de las comunidades (Escudero & Valladares, 2016; Weiher et al., 2011; Shipley, 2010; Vellend, 2010; Lortie et al., 2004).

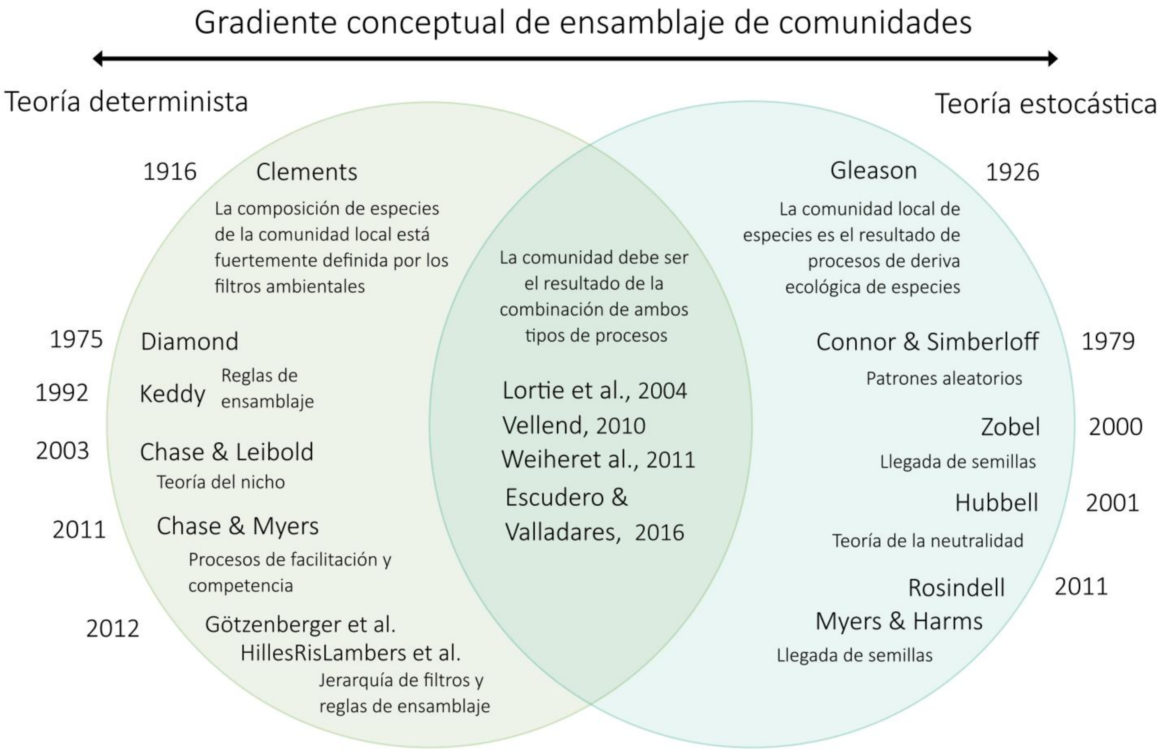

Figura 1. Esquema de la evolución de las diferentes teorías y ejemplos de trabajos que han tratado a lo largo de la historia de explicar los diferentes procesos que forman parte del ensamblaje de comunidades vegetales.

Reglas de ensamblaje de comunidades

La teoría de la coexistencia de especies (Götzenberger et al., 2012; HilleRisLambers et al., 2012; Keddy, 1992) expone que la composición de una comunidad vegetal local viene determinada por cualquier proceso ecológico que seleccione las especies a favor o en contra de un conjunto regional de especies. Las reglas de ensamblaje actuarían por tanto de manera jerárquica a diferentes escalas biológicas y geográficas a través de procesos de dispersión de semillas, las condiciones abióticas y las interacciones bióticas (Götzenberger et al., 2012; Luzuriaga et al., 2012, 2015; Agrawal et al., 2007; Zobel, 1997), determinando finalmente la estructura y composición de la comunidad.

A gran escala, son los procesos biogeográficos, junto con los procesos de especiación y extinción, son los encargados de estructurar el conjunto regional de especies (Pausas & Verdú, 2010). A su vez, a escala local, los procesos ecológicos actuarían retroalimentando e influyendo en la composición y diversidad del conjunto regional de especies (Pausas & Verdú, 2010). Tradicionalmente, se ha propuesto que los dos principales procesos ecológicos que estructuran y forman las comunidades ecológicas son la competencia y el filtrado de hábitats (Weiher & Keddy, 1995; Wilson, 1999). Ya Darwin (1859), propuso que las especies que comparten género suelen ser más parecidas física y estructuralmente y que por ello la competencia entre ellas será más fuerte que entre especies de distinto género (Pausas & Verdú, 2010). Aunque en los últimos años también se ha puesto el foco de atención en los procesos de facilitación (Madrigal-González et al., 2020; Brooker et al., 2008; Gómez-Aparicio et al., 2004). A partir de estos postulados se han desarrollado numerosos estudios tratando de entender los diferentes mecanismos que subyacen al proceso de ensamblaje de especies.

También es importante la escala a la que analizamos los procesos de ensamblaje como apuntan diferentes estudios (Cadotte et al., 2009; Emerson & Gillespie, 2008; Graham & Fine, 2008; Kraft et al., 2007; Cavender-Bares et al., 2006). En este trabajo nos vamos a centrar en el estudio de una comunidad a escala local. Los factores ambientales influyen en la composición de una determinada comunidad local al actuar como filtro, seleccionando las especies con mejores adaptaciones a las condiciones locales (Chase & Leibold, 2003). Estos filtros ambientales, no actuarían como mecanismos de todo o nada, sino como filtros probabilísticos (Shipley, 2010) afectando de manera diferente al éxito de cada especie dependiendo de unas determinadas condiciones (Luzuriaga et al., 2015). Los responsables de este filtrado ambiental de especies son tanto los componentes abióticos (Kraft et al., 2015) como los componentes bióticos (Götzenberger et al., 2012; Luzuriaga et al., 2012, 2015) presentes en el sistema. Por lo tanto, las condiciones abióticas y las interacciones bióticas serán clave para el establecimiento de las especies de esta localidad concreta y determinaran los mecanismos del ensamblaje final (Luzuriaga et al., 2012; Emerson & Gillespie, 2008; Michalet et al., 2006; Shipley, 2010). Las condiciones abióticas tienden a seleccionar a las especies en función de su capacidad para colonizar, establecerse y persistir en un contexto abiótico determinado, mientras que, las interacciones bióticas tienden a seleccionar a las especies en función de las relaciones con otras especies competidoras, mutualistas y consumidoras que estén presenten en la localidad (Weiher et al., 2011).

Nuestro sistema de estudio

La comunidad ecológica que hemos seleccionado para este estudio es la formada por la comunidad vegetal que aparece en los sistemas yesíferos del centro de la península ibérica. Los yesos son suelos restrictivos que albergan un conjunto florístico excepcional, así como algunos de los puntos de biodiversidad más importantes de los ecosistemas terrestres (Mota et al., 2011; Harrison & Inouye, 2002). Además, previos estudios ya han utilizado esta comunidad como objeto de estudio confirmando que presenta un marco ideal para la evaluación de los procesos de ensamblaje de comunidades (Sánchez et al., 2022; Peralta et al., 2019; Luzuriaga et al., 2012, 2018, 2020; Escudero et al., 2015).

Componentes abióticos y bióticos de nuestro sistema

Las comunidades vegetales de estos sistemas tienen que hacer frente a un componente abiótico regional muy fuerte debido tanto a las condiciones climáticas como edáficas. Estos sistemas se caracterizan por presentar una sequía estival muy marcada alcanzando temperaturas extremadamente altas. Además, las condiciones edáficas presentan unas características químicas y físicas muy restrictivas (Escudero et al., 2015). La disponibilidad de agua, tanto la cantidad como la temporalidad, viene determinada por la elevada variabilidad interanual de las precipitaciones anuales (Luzuriaga et al., 2012, 2015), por lo tanto, la disponibilidad de agua sería el primer filtro al que tendrían que hacer frente el conjunto regional de especies (Luzuriaga et al., 2012).

Como ya hemos señalado, los componentes bióticos desempeñan un papel fundamental en la formación de las comunidades. En nuestro sistema yesífero del centro peninsular los componentes bióticos más destacados son la presencia de costras biológicas en el suelo (CBS) y la gramínea perenne de gran tamaño *Macrochloa tenacissima* (Luzuriaga et al., 2012; Maestre et al., 2001, 2003; 2007; Maestre & Cortina, 2005). Las costras biológicas del suelo (CBS) son complejas combinaciones de cianobacterias, líquenes, musgos, algas, hongos y microartrópodos que están íntimamente asociados a las partículas del suelo o en los primeros centímetros de éste (Belnap et al., 2016). La CBS participa en diferentes procesos: en la infiltración y evapotranspiración del agua del suelo (Berdugo et al., 2014; Chamizo et al., 2012; Maestre et al., 2002); en el ciclo del nitrógeno (Belnap, 2002; Castillo-Monroy et al., 2010; Delgado-Baquerizo et al., 2010; Elbert et al., 2012; Harper & Belnap, 2001); en la estabilización del suelo (Bowker et al., 2011; Chaudhary et al., 2009); en la descomposición de la hojarasca (Berdugo et al., 2021) etc. Además, se ha demostrado su relevancia en diferentes etapas de la vida de las plantas anuales, cómo en la formación del banco de semillas, Peralta et al., 2016; germinación y establecimiento de las plántulas, Ortiz et al., 2023; Escudero et al., 2007; Romão & Escudero, 2005; Meyer, 1986; o en el desarrollo de la planta y su fenología, Luzuriaga et al., 2012, 2015.

La presencia de grandes macollas de *Macrochloa tenacissima* es otro de los componentes bióticos relevantes en nuestro sistema. Los parches de vegetación formados por la presencia de esta gramínea de gran porte presentan una fuente de heterogeneidad ambiental muy importante en sistemas áridos (Maestre & Escudero, 2009). La presencia de *M. tenacissima* modifica el contenido de nutrientes, materia orgánica, intensidad lumínica, temperatura y disponibilidad de agua (Zamora et al., 2008). Además, algunos estudios también apuntan a que *M. tenacissima* actúa como planta nodriza aumentando la riqueza de especies y promoviendo la creación de microhábitats (Pugnaire et al., 2004) y reduciendo la temperatura del suelo (Maestre et al., 2001).

Tanto la CBS como *Macrochloa tenacissima* han sido objeto de estudio de numerosos trabajos por su conocida relevancia en el proceso de ensamblaje de comunidades. Sin embargo, cuesta encontrar trabajos manipulativos que permitan aislar el efecto de cada uno de estos elementos (ver Maestre et al., 2011,2001; Cortina et al., 2010).

Enfoque taxonómico, funcional y filogenético

El número de herramientas de análisis que los ecólogos de comunidades tienen a su disposición ha aumentado notablemente durante los últimos años. La diversidad de especies puede cuantificarse utilizando diferentes métodos: contando el número de especies presentes, es decir la riqueza de especies (diversidad taxonómica); cuantificando los diferentes rasgos funcionales de esas especies (diversidad funcional) o utilizando secuencias genéticas para conocer la divergencia evolutiva de los linajes de especies presentes en la comunidad (diversidad filogenética) (Staab et al., 2021; Tucker et al., 2017; Cadotte et al., 2009). El uso de la riqueza de especies, a pesar de ser uno de los métodos más utilizados (Gotelli & Colwell, 2001), no tiene en cuenta las diferencias evolutivas y ecológicas entre especies (Safi et al., 2011), aunque hay autores que mantienen que es la identidad de las especies la que mejor explica las interacciones de competición y facilitación (Venail et al., 2014). Por otro lado, el uso de los rasgos funcionales para entender el éxito de ciertas especies sobre otras en determinadas condiciones ambientales ha sido ampliamente desarrollado durante los últimos años (de Bello et al., 2015; Götzenberger et al., 2012; S. Lavorel & Garnier, 2002). Por su parte la diversidad filogenética está empezando a postularse como una alternativa para comprender la presencia y coexistencia de ciertas especies en condiciones ambientales determinadas (Chaves et al., 2021; Cadotte et al., 2008; Kraft et al., 2007).

Los rasgos funcionales son expresiones del fenotipo que nos indican las estrategias ecológicas de las plantas para el uso de recursos, crecimiento, distribución y adaptación a las condiciones ambientales (Westoby & Wright, 2006). La diversidad funcional representa la variedad de estos rasgos funcionales que presentan las especies de una comunidad (Flynn et al., 2011). La respuesta de la diversidad funcional de una comunidad ante un estrés ambiental puede ser la selección de especies que presenten los rasgos funcionales mejor adaptados a ese entorno, produciéndose, por tanto, una “convergencia funcional” de la comunidad (Weiher et al., 2011). Sin embargo, la respuesta al estrés abiótico también podría dar como resultado un conjunto de especies con diferentes estrategias contra ese estrés, lo que se traduciría en una comunidad con una alta diversidad funcional o “divergencia funcional” (Funk et al., 2017). Ante un fuerte filtrado biótico, si los rasgos funcionales reflejan diferencias en el nicho de las especies, se espera que se produzca una divergencia de los rasgos funcionales de las especies presentes en el sistema (Funk et al., 2017; Weiher et al., 2011) ya que la exclusión competitiva (sensu Hardin, 1960) promovería la diferenciación de nicho (Mason et al., 2005). Por otro lado, si los rasgos funcionales están relacionados con la capacidad competitiva de las especies, se espera una convergencia dentro de la comunidad, promovida por el equilibrio de simetrías competitivas, y por tanto una baja diversidad funcional (Mayfield & Levine, 2010).

La diversidad filogenética refleja la diversidad de roles ecológicos y nos informa además de la historia evolutiva de las especies que coexisten en una comunidad (Muñoz et al., 2017; Cadotte et al., 2008; Emerson & Gillespie, 2008). Como ocurría con la diversidad funcional, con la diversidad filogenética también podemos encontrar patrones opuestos de la comunidad en respuesta al filtrado ambiental. Ante un fuerte estrés ambiental, cabría la posibilidad de que se produjera una "convergencia filogenética", es decir, una baja diversidad filogenética de la comunidad. Esto podría deberse a que los rasgos funcionales más relevantes para la adaptación de las especies a ese estrés ambiental y la capacidad competitiva se conservan a lo largo de la filogenia, es decir, las especies emparentadas serían más similares entre sí. (Emerson & Gillespie, 2008; Cavender-Bares et al., 2004; Webb, 2000). También podría darse el caso de que la señal filogenética de un rasgo fuese baja, en ese caso se produciría una divergencia filogenética seleccionando especies más distantes, pero con valores del rasgo adaptados a las condiciones (Cavender-Bares et al., 2004). Por otro lado, si ante un filtro biótico el mecanismo de ensamble que predomina es el de la exclusión competitiva, se produciría una "divergencia filogenética" o baja diversidad filogenética de la comunidad (Mayfield & Levine, 2010; Emerson & Gillespie, 2008).

Objetivos

Con este estudio pretendemos identificar y evaluar los principales componentes que intervienen en el proceso de ensamblaje de una comunidad dominada por plantas anuales en un ecosistema semiárido (Figura 2). Para poder abordar este objetivo principal, a lo largo de cuatro capítulos iremos centrándonos en diferentes componentes de nuestro sistema y en los mecanismos de ensamblaje más relevantes en nuestra comunidad:

- En el capítulo 1 trataremos de definir tanto la contribución relativa de los procesos deterministas -representados principalmente por el filtrado biótico- como la contribución de los procesos estocásticos- definidos principalmente por la llegada de propágulos- a la formación de las comunidades vegetales locales en nuestro sistema. Trataremos de contribuir de esta forma a determinar el lugar que corresponde al proceso de ensamblaje en el gradiente conceptual generado a partir de las teorías de Clements y Gleason (Figuras 1 y 2). Además, desde un enfoque funcional, analizaremos los principales rasgos que presentan nuestra comunidad para identificar los mecanismos causales que operan en el proceso de ensamblaje de nuestra comunidad.
- En el capítulo 2 nos centraremos en uno de los factores bióticos más relevantes de nuestra comunidad, la presencia de *Macrochloa tenacissima*. Estudiaremos por separado los efectos de las partes aéreas y subterráneas de esta especie, considerada como una planta facilitadora (planta nodriza) en sistemas de estudio como el nuestro. También estudiaremos qué ocurre al relajar el componente abiótico más relevante en estos sistemas (estrés hídrico) y el efecto de la disponibilidad de semillas. Analizaremos también los rasgos funcionales de las especies para estudiar el posible efecto filtrador o facilitador de *M. tenacissima.*
- En el capítulo 3 nos centraremos en otro de los factores bióticos relevantes de nuestro sistema, la costra biológica del suelo (CBS). Trataremos de determinar los efectos de la CBS sobre el establecimiento y el desarrollo de las especies de plantas coexistentes manipulando la diversidad funcional (DF) inicial de las comunidades de plantas seleccionadas. Para crear las diferentes combinaciones de plantas de alta y baja diversidad funcional hemos seleccionado el rasgo altura máxima de la planta (MPH).
- En el capítulo 4, manipularemos tanto la diversidad funcional (DF) inicial como la diversidad filogenética (DP) inicial de nuestros conjuntos experimentales de plantas anuales. Con ello, pretendemos desvelar la contribución relativa de la estructura funcional y filogenética de las especies coexistentes en los procesos de ensamblaje. Estudiaremos de esta forma los efectos tanto independientes como interactivos de la DF y DP sobre el desarrollo de las plantas anuales de nuestro sistema.

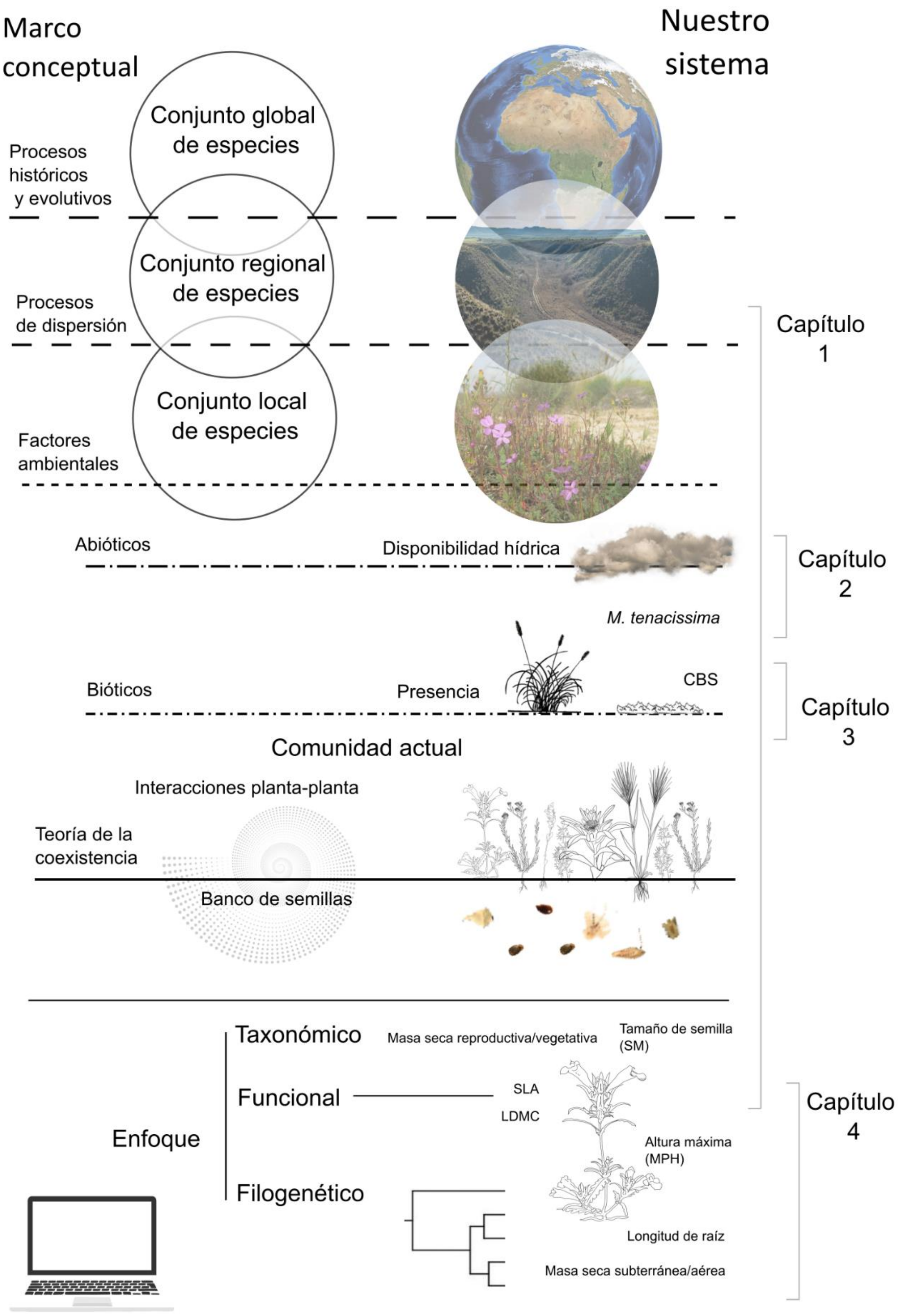

Figura 2. Esquema resumen del marco conceptual de este trabajo, nuestro sistema de estudio y las partes que engloba cada capítulo.

Metodología

Zona de estudio

Como objeto de estudio hemos seleccionado las comunidades vegetales dominadas por plantas anuales de un sistema yesífero localizado en el centro peninsular, más concretamente en el valle central del río Tajo. El clima mediterráneo semiárido que presenta nuestra zona de estudio se caracteriza por una temperatura media anual de 15 °C, y una precipitación media anual de 365 mm^{-2} $año^{-1}$ (Estación meteorológica de Getafe, 40°17′58′′N; 3°43′20′′E; 620 m). Las precipitaciones se concentran a finales de otoño y a principios de primavera, presentando una fuerte sequía estival. La vegetación que encontramos está formada por *Macrochloa tenacissima* (L.) Kunth. y otros arbustos gipsófilos de bajo porte (*Lepidium subulatum* L.*, Centaurea hyssopifolia* Vahl., *Gypsophila struthium* L. y Helianthemum squamatum (L.) Dum. Cours.), además de una rica comunidad efímera de plantas anuales (alrededor de 120 especies; (Luzuriaga et al., 2012, 2015, 2018, 2020) entre las que podemos encontrar *Chaenorhinum r*eyesii (C. Vicioso & Pau) Benedí, *Festuca gypsophila* (Hack.) Paunero, *Campanula fastigiata* Dufour ex Schult, *Alyssum simplex* Rudolphi, *Cerastium glomeratum* Thuill, *Filago pyramidata* L. y *Reseda stricta* Pers. Encontramos también una costra biológica del suelo (CBS) compuesta en su mayoría por líquenes (*Diploschistes diacapsis* (Ach.) Lumbsch y *Squamarina lentigera* (G.H. Weber) Poelt, principalmente).

Experimentos de campo e invernadero

Para abordar todos los objetivos planteados en esta tesis se han realizado manipulaciones experimentales de la comunidad seleccionada tanto en campo (capítulos 1 y 2) como en invernadero (capítulos 3 y 4). Este enfoque experimental nos va a permitir conocer las relaciones causa-efecto de los principales componentes de este sistema (Figura 3).

Los experimentos de campo se han desarrollado en la Estación Experimental de Sotomayor localizada en Aranjuez (40°01′55.7″N - 3°32′48.3″W, 590 m). Las características de esta zona son las indicadas anteriormente. Los experimentos se realizaron en una superficie de 2710 m^2 en una superficie plana y vallada para evitar las interacciones con herbívoros comunes en la zona, como conejos. El primer experimento de campo (capítulo 1) consistió en: dos tratamientos para evaluar los efectos de la llegada de propágulos (parcelas con suelo libre de semillas vs. parcelas con suelo natural homogeneizado con presencia de banco de semillas completo) combinados con tres tratamientos para evaluar el efecto de los principales componentes bióticos del sistema (parcelas con presencia de CBS, con presencia de *Macrochloa tenacissima* y parcelas con suelo desnudo). El resultado es un diseño factorial completo con seis tratamientos experimentales que replicamos 10 veces, un total de 60 parcelas. Este experimento tuvo un seguimiento de cuatro años.

El segundo experimento de campo (capítulo 2) consistió en: tres tratamientos para evaluar el efecto de *Macrochloa tenacissima* y sus diferentes partes (plantas intactas *vs.* solo la parte de arriba *vs*. solo la parte subterránea) además de parcelas control sin presencia de *M. tenacissima*, combinados con dos tratamientos de disponibilidad hídrica (parcelas con precipitación natural *vs*. parcelas con precipitación natural además de riego manual) y con dos tratamientos para evaluar los efectos de la llegada de propágulos (parcelas con suelo libre de semillas vs. parcelas con suelo natural homogeneizado con presencia de banco de semillas completo). El resultado es un diseño factorial completo con 16 tratamientos experimentales replicados 10 veces, un total de 160 parcelas. Aunque este experimento tuvo un seguimiento de tres años, solo evaluamos el último.

Los experimentos en invernadero se han desarrollado utilizando la técnica de jardín común o “common garden”. Esta técnica nos permite recrear nuestras comunidades en macetas y replicarlas para poder aplicarles los tratamientos seleccionados bajo condiciones controladas. El primer experimento en invernadero (Capítulo 3) consistió en la creación de ensambles manipulando la diversidad funcional inicial de nuestra comunidad. Para ello seleccionamos el rasgo altura máxima de la planta (MPH, máximum plant height) y creamos combinaciones de especies de plantas anuales: sólo especies de plantas grandes, sólo especies de plantas pequeñas y especies de plantas de diversos tamaños. Las combinaciones experimentales de plantas anuales con alta diversidad funcional (DF) inicial están compuestas por especies coexistentes con diferentes tamaños máximos. Del mismo modo, las combinaciones de baja DF inicial están compuestas por especies coexistentes con tamaños máximos grandes o pequeños. Para cada combinación seleccionamos dos grupos diferentes de plantas. Estas tres combinaciones las cruzamos con tres tratamientos para evaluar el efecto de la CBS (macetas con presencia de CBS intacta, con presencia de CBS perturbada físicamente o macetas sin presencia de CBS). El resultado es un diseño factorial con 18 escenarios distintos replicados 15 veces, un total de 270 conjuntos experimentales (macetas). Este experimento tuvo una duración de un año.

El segundo experimento en invernadero (capítulo 4) consistió en la creación de 11 combinaciones de plantas en las que manipulamos su diversidad filogenética inicial. A su vez, estas combinaciones presentan diferentes valores de diversidad funcional inicial. Cada uno de estos escenarios se combinó con dos tratamientos de disponibilidad hídrica (precipitación media mensual vs. un tercio de la precipitación medía, sequía). El resultado son 22 escenarios replicados 12 veces, un total de 264 conjuntos experimentales (macetas). Este experimento tuvo una duración de un año.

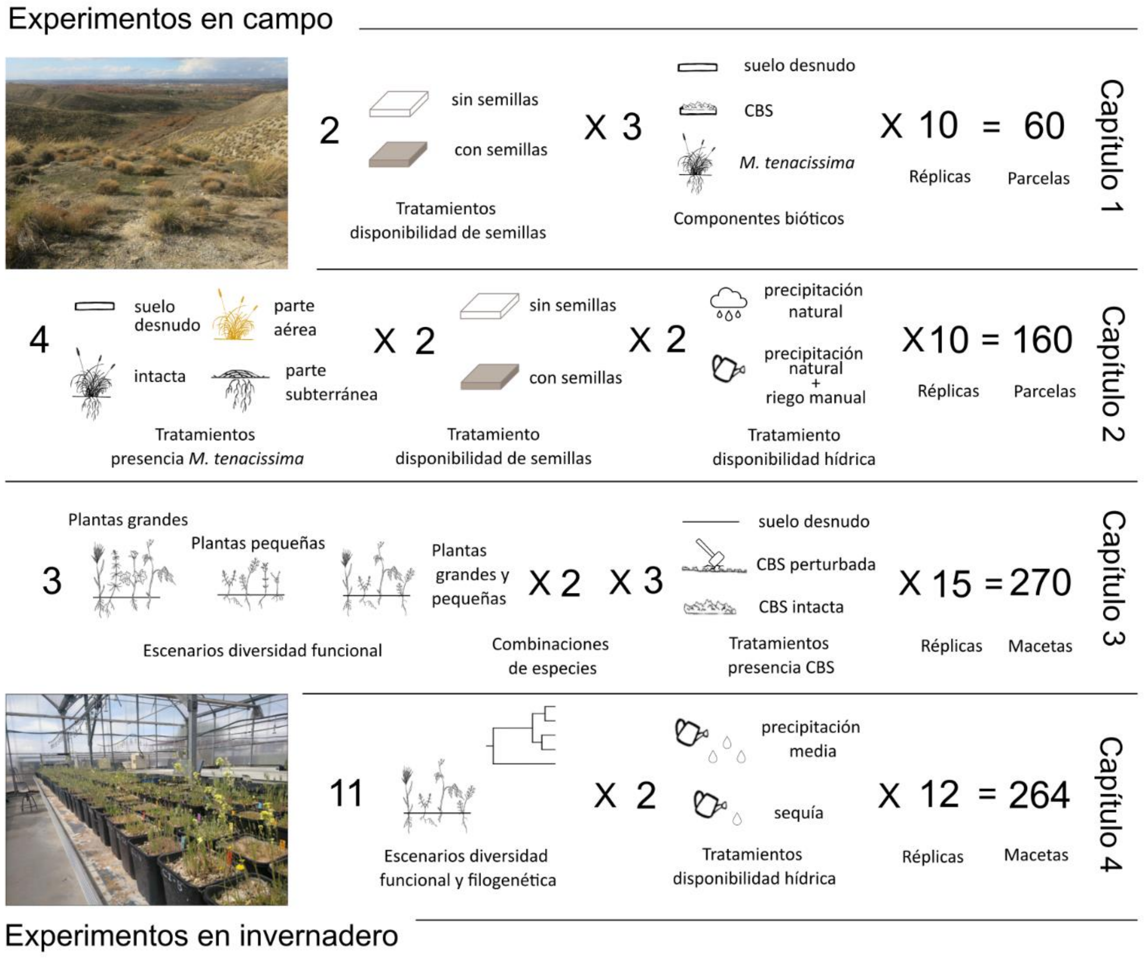

Figura 3. Esquema de los cuatro experimentos desarrollados en esta tesis.

Herramientas de análisis

Tanto para la creación de las combinaciones de especies (capítulo 3 y 4) como para el análisis de las características de las comunidades formadas (capítulo 1 y 2) hemos utilizado una base de datos que contempla los rasgos funcionales de las especies que forman nuestra comunidad. Esta base de datos fue creada por Peralta et al., (2019) y contiene información sobre los rasgos funcionales relacionados con estrategias ecológicas fundamentales (Westoby, 1998): área foliar específica (SLA; la relación entre el área foliar y la masa seca foliar); contenido de materia seca foliar (LDMC; la relación entre la masa seca foliar y la masa fresca); relación raíz:tallo (raíz/tallo; es decir, proporción reproductiva (rep./veg.; es decir, proporción de masa seca reproductiva:vegetativa); altura máxima de la planta (MPH; es decir, estatura de la planta sin las inflorescencias) y masa de la semilla (SM; peso seco de la semilla).

Para todos los análisis estadísticos hemos utilizado el entorno de desarrollo *Rstudio,* que mediante el lenguaje de programación R nos ha permitido realizar todos los análisis y gráficos que forman esta tesis. Los índices que hemos utilizado para cuantificar la diversidad taxonómica de nuestras comunidades han sido: riqueza de especies, el porcentaje de cobertura total de plantas, el índice inverso de Simpson y el cálculo de la equitatividad. Para evaluar la composición de las especies se han utilizado PERMANOVAS y NMDS. Para cuantificar la diversidad funcional hemos utilizado el índice de Rao, el CWM y el MPD y para cuantificar la diversidad filogenética el PSV. Además, hemos realizado glm y glmms para analizar la respuesta de la comunidad a nuestros diferentes tratamientos.

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CAPÍTULOS/CHAPTERS

CHAPTER 1

Assessing the contribution of deterministic *vs.* stochastic processes to local species assembly: a field experiment with annual-dominated plant communities in gypsum systems

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ABSTRACT

Understanding the processes involved in the formation of communities is still a hot topic with many unresolved questions. Assembly of plant communities is generally approached within the frame of a conceptual gradient defined by two opposing postulates: the deterministic approach (Clements, 1916), which interprets the community as a constrained combination of species strongly defined by environmental filters, and the stochastic view (Gleason, 1926), which interprets the community as an open, randomly coinciding combination of species, subordinated to ecological-drift processes. Although both approaches have received much attention, assembly theory has grown mainly based on observational studies due to the difficulty of manipulating entire communities. In this study, we proposed a novel field experiment in a semi-arid Iberian gypsum system to evaluate the relative contribution of both stochastic processes (here represented with the arrival of propagules) biotic (represented with the presence of perennials and biological soil crust) and abiotic (yearly rainfall) environmental filtering to the assembly of the annual plant dominated species communities. The field experiment consisted of two treatments of soil seed availability to test the effects of arrival of propagules (i.e., soil free of seeds *vs*. homogenised natural soil with the complete seed bank) combined with three treatments testing the effects of the main biotic components of the system (i.e., presence of biological soil crusts –BSC– *vs*. presence of *Macrochloa tenacissima* tussocks *vs*. open areas) on plant assembly, resulting in a complete factorial design with 6 experimental treatments 10-fold replicated (i.e., 60 plots). Plant assemblages in plots were assessed during four consecutive years. Our results demonstrated that, in years with average or above rainfall amounts, stochastic processes dominated over deterministic processes in species assembly processes. Although environmental factors affected plant cover and taxonomic diversity, they did not generate selection of species based on their traits (specific leaf area, SLA; leaf dry matter content, LDMC; root:shoot ratio; reproductive ratio; maximum plant height, MPH; and seed mass, SM). Furthermore, the role played by the presence of BSC on community assemblage should be highlighted, as their presence increased richness, total cover, and taxonomic diversity even in initial seed free soil conditions.

Keywords

Annual plants, biotic filters, climatic variability, community assembly, deterministic processes, environmental filters, functional diversity, functional traits, stochastic processes, taxonomic diversity.

INTRODUCTION

The processes involved in community assembly are a long-standing issue in community ecology. A conceptual gradient from deterministic (Clements, 1916) to stochastic (Gleason, 1926) theory has been generated. Clements (1916) suggested that only certain combinations of species can occur in nature. Thus, according to the Niche Theory (Hutchinson, 1957) communities would be organised based on assembly rules, such as facilitative and/or competitive interactions among species. On the other hand, stochastic processes, among which the arrival of propagules to the system is crucial , imply that the community is simply a coincidence of species (Myers & Harms, 2011; Zobel et al., 2000). Furthermore, environmental heterogeneity is expected to play a crucial role (Chase & Myers, 2011). Nowadays, there is a generalized consensus that both deterministic and stochastic processes contribute to the formation of communities (Escudero & Valladares, 2016; Weiher et al., 2011; Vellend, 2010; Lortie et al., 2004), on the basis of a new, integrative view unifying different coexistence theories such as niche theory (Chase & Leibold, 2003) and neutrality theory (Hubell, 2001)(Wang et al., 2018; Furniss et al., 2017; Chase, 2014; Holt, 2006; Tilman, 2004).

Several studies suggest that realised assemblages are ultimately the result of environmental filters acting in a hierarchical manner (Götzenberger et al., 2012; Luzuriaga et al., 2012, 2015; Agrawal et al., 2007; Zobel, 1997). Firstly, evolutionary processes impose long lasting selection of species, which eventually define the regional species pools. Subsequently, environmental abiotic (sensu Kraft et al., 2015) and biotic drivers (Götzenberger et al., 2012; Luzuriaga et al., 2012, 2015) would select the species which in fact will participate in the realized assemblages. Furthermore, stochastic processes related to ecological drift and seed arrival would act simultaneously with assembly rules (Myers & Harms, 2011; Zobel et al., 2000). Although both approaches (deterministic *vs.* stochastic) have received much attention of community ecologists, being profusely theorized (e.g., Rosindell et al., 2011; Hubbell, 2001; Diamond, 1975), there is still a lack of definite information concerning the actual contribution of both kinds of processes to plant community assembly.

Species in local assemblages are decisively filtered by environmental factors that select those with better adapted traits to the local conditions (Chase & Leibold, 2003). Environmental filters, however, do not operate as an all-or-nothing mechanism, but rather as probabilistic filters (Shipley, 2010) that affect differently the probability of each species to succeed in the community, depending on the particular conditions at a given time and space (Luzuriaga et al., 2015). Mediterranean gypsum steppe communities are subjected to very strong regional abiotic filtering: summer drought along with extremely high temperatures and restrictive chemical and physical soil conditions (Escudero et al., 2015). These stressful conditions make small-scale biological filtering processes particularly active and exacerbated, and take special relevance in the determination of realised assemblages through processes of competition, facilitation, or inhibition (Rubio, et al., 2023; Sánchez et al., 2022; Peralta et al., 2019; Luzuriaga et al., 2012, 2018, 2020; Escudero et al., 2015). Furthermore, gypsum systems often comprise highly dynamic and species-rich annual communities with a relevant participation to soil seed banks (Peralta et al., 2016). All these features offer an ideal framework to assess the actual contribution of both deterministic and stochastic processes to the conformation of plant communities.

Taxonomic combinations in realized assemblages will ultimately depend on the dispersal ability of species participating in the regional pool (Götzenberger et al., 2012; Vellend, 2010). In the Iberian gypsum systems, soil seed banks are well- structured, relatively homogeneous and abundant, with densities ranging from 15000 to 21000 seeds/m^2 belonging up to 70 species in the few upper soil centimetres (Caballero et al., 2003; 2008a). The recruitment conditions in these stressful environments are unpredictable, thus soil seed banks are critical for the maintenance of plant communities (Olano et al., 2012; Thompson & Ban., 1997). Most of the dominant annual plants in gypsum systems do not have specialized dispersal mechanisms (i.e. athelechory sensu Ellner & Shmida, 1981), thus seeds mainly remain in the vicinity of their mother plants (Peralta et al., 2023) and secondary dispersal may transport seeds to nearby bare soil areas (Escudero et al., 2015; Olano et al., 2005, 2012), so species composition in aboveground vegetation and soil seed banks tend to be highly correlated (Rubio et al., 2023; Peralta et al., 2016; Martinez-Duro et al., 2012; Caballero et al., 2008b) in space and time in these systems, as properly explained by the 'spiral dynamics model' (Caballero et al., 2008b). Therefore, changes in aboveground vegetation will influence the soil seed bank that in turn will determine the aboveground vegetation of the next growing season. Furthermore, soil seed banks in these systems recover quickly after destruction (Escudero et al., 2015; Martinez-Duro et al., 2012; Olano et al., 2012). This recovery is based mainly on the seed rain at small scales together with secondary dispersal from intact seed banks in the vicinity (Olano et al., 2012). However, the importance of seed availability in the process of plant community formation remains poorly understood.

Biotic factors can play a core role in the organization of plant communities in gypsiferous steppes of the central Iberian Peninsula. There, *Macrochloa tenacissima* (L.) Kunth perennial grass tussocks and biological soil crusts (BSC) are biotic components which decisively affect the establishment of plant species. *Macrochloa tenacissima* is a major plant component having a main impact on ecological processes and structure of annual plant communities in Mediterranean gypsum systems (Luzuriaga et al., 2012; Maestre et al., 2007; Maestre & Cortina, 2003), due to their abundance, resistance to stressful conditions, resprouting ability, and the vegetative centrifuge propagation of stems, which results in large-diameter grass tussocks (up to 1 m), being up to 1 m tall (Maestre et al., 2007). Previous studies in gypsum soil systems point to an amelioration of environmental conditions related to the presence of *Macrochloa*, resulting in higher plant productivities nearby tussocks, but with no positive effects on richness and taxonomic diversity (Luzuriaga et al., 2012). However, other studies found that *M. tenacissima* can act as nurse plants, increasing richness and promoting microhabitat segregation (Pugnaire et al., 2004). Vegetation patches created by *Macrochloa* tussocks represent the greatest source of environmental heterogeneity in semi-arid systems (Maestre & Escudero, 2009), modifying nutrient, organic matter contents, light intensity and the amount of photosynthetically active radiation, temperature, and water availability in their vicinity (Zamora et al., 2008; Maestre et al. 2001). Moreover, *M.*

tenacissima can exert a direct effect on soil seed bank properties by trapping seeds under their canopies during primary or secondary dispersion events (Bullock & Moy, 2004). Furthermore, soil moisture under *M. tenacissima* is usually higher than in bare soil (Maestre et al., 2003; Maestre & Cortina, 2003). Another important biotic factor in semi-arid environments is the presence of well-conserved BSC, whose effect is largely documented (Belnap et al., 2003; 2016). Biological soil crusts are complex combinations of cyanobacteria, lichens, mosses, algae, fungi, and microarthropods that are intimately associated with particles within the top few centimetres of the soil surface (Belnap et al., 2016).This living layer is also a major source of environmental heterogeneity in drylands (e.g., Belnap et al. 2016; Concostrina-Zubiri et al., 2013) throughout its participation in crucial processes for plant life at fine spatial scales: water soil infiltration and evapotranspiration (Berdugo et al., 2014; Chamizo et al., 2012; Maestre et al., 2002); nitrogen cycle (Elbert et al., 2012; Castillo-Monroy et al., 2010; Delgado-Baquerizo et al., 2010; Belnap, 2002; Harper & Belnap, 2001); soil stabilization (Bowker et al., 2011; Chaudhary et al., 2009); or litter desomposition (Berdugo et al., 2021). In gypsum systems, BSC can act as a physical barrier for seedling establishment (Ortiz et al., 2023; Escudero et al., 2007; Romão & Escudero, 2005; Meyer, 1986), facilitating however growth and fitness of plants that surpass restrictions in early life-cycle phases (Ortiz et al., 2023). Several studies have proven the relevance of BSC in different life stages for annual plants (e.g., seed bank formation, Peralta et al., 2016; seed germination and seedling establishment, Escudero et al., 2007; plant development and phenological peak, Luzuriaga et al., 2015, 2012).

In this work we aimed to define both the relative contribution of stochastic processes –represented by the seed arrival in our study– and that of deterministic processes –represented by biotic environmental filtering in our study– to the local conformation of plant communities in gypsum steppes, to realistically locate the assembly process on the Clements' and Gleason's conceptual gradient and to better understand the mechanisms organizing those communities. For this purpose, in a four-year lasting field experiment in a gypsum system in the centre of the Iberian Peninsula, we manipulated the initial availability of seeds in the soil (complete seed bank *vs.* seed free soil), along with the biotic filters (presence/absence of *Macrochloa* tussocks and biological soil crusts) in a full factorial design, and analysed their effects on the resulting plant assemblages, dominated by annual species. Climate in the Mediterranean gypsum systems greatly varies from year to year (e.g., Luzuriaga 2015, 2012), so annual plant composition and community structure usually vary yearly. Moreover, the effects of both perennial plants (*Macrochloa* tussocks) and BSC on the annual species community depend on the abiotic component (water availability) (Luzuriaga et al., 2012). For that reason, we recorded the combined effects of seed arrival and key biotic factors on species composition, richness, total cover, and functional diversity in plant assemblages during four consecutive years (2019, 2020, 2021 and 2022). Functional facet may significantly contribute to identify causal mechanisms operating in the community assembly. In recent times plant-trait based approaches have positioned as powerful tools to study fundamental questions in ecology (Escudero & Valladares, 2016). Identifying functional patterns in realised assemblages help us to understand the filtering effects of environmental factors operating in a system (Shipley, 2010; Suding et al., 2008; McGill et al., 2006). Intense abiotic conditions select species with traits adapted to cope them, resulting in functional convergence (Funk et al., 2017) in the realized species assemblage. On the other hand, functional divergence is expected when competition is the main restrictive force due to limiting similarity (Funk et al., 2017; Weiher et al., 2011). For the purpose of studying the predominant mechanisms in our community, we selected major functional traits related to the leaf economics spectrum (specific leaf area (SLA) and leaf dry matter content (LDMC)), reproduction trade-offs (seed mass and reproductive ratio), establishment of size hierarchies (maximum plant height), and resource uptake (root:shoot dry mass ratio)(Cornelissen et al., 2003). To the best of our knowledge, no previous studies have evaluated the joint effects of abiotic (year to year climate conditions) and biotic filters (BSC and *M. tenacissima*) on the formation of plant communities under field conditions simultaneously considering seed availability in the soil.

We aimed to test the following hypotheses on the contribution of stochastic and deterministic processes to the conformation of annual-dominated plant communities in semiarid gypsum systems (Figure 1): (1) if during plant assembly the contribution of stochastic processes prevails over deterministic environmental filters, we should expect that no functional trait selection would occur, leading to random functional patterns in the resulting species assemblages. We expect that this hypothesis will fulfil in seed-free soil scenarios, where seed primary and secondary dispersal would be the main ecological processes driving species assembly; (2) if the presence or absence of biotic components of arid systems (BSC and *Macrochloa* tussocks) create restrictive microenvironments, especially in dry years (Sánchez et al., 2022; Peralta et al., 2019; Luzuriaga et al., 2012), we may expect that community assembly would be driven by the selection of species with adapted traits to cope with those conditions, consequently resulting in functional convergence; (3) if biotic components of arid systems (BSC and *Macrochloa* tussocks) ameliorate environmental conditions resulting in high biomass production of annual plant assemblages, it would enhance competitive interactions among coexisting species (Boeken, 2018; Bergholz et al., 2017; Tielbörger & Kadmon, 2000; Kadmon & Shmida, 1990), and we expect that the limiting similarity principle will act during the assembly process leading to functional divergence in the resulting plant communities; (4) if biotic components create milder conditions but not to the extreme of triggering competitive interactions among coexisting species, we may expect stochasticity to prevail, because in mild environments without significant competition among species, any species present in the soil seed bank could potentially succeed; (5) Year to year climate variability may determine shifts in the intensity of abiotic filtering, and of biotic interactions. Thus, if climatic conditions enhance abiotic stress, then functional patterns will move towards functional convergence; on the contrary, if climate conditions increase biomass productivity and enhance intensity of competitive relationships among species then we may expect that functional patterns would shift towards functional divergence in the resulting assemblages; and if climate conditions are in the range of physiological tolerance of species we may expect that stochastic processes will prevail leading to random assemblages.

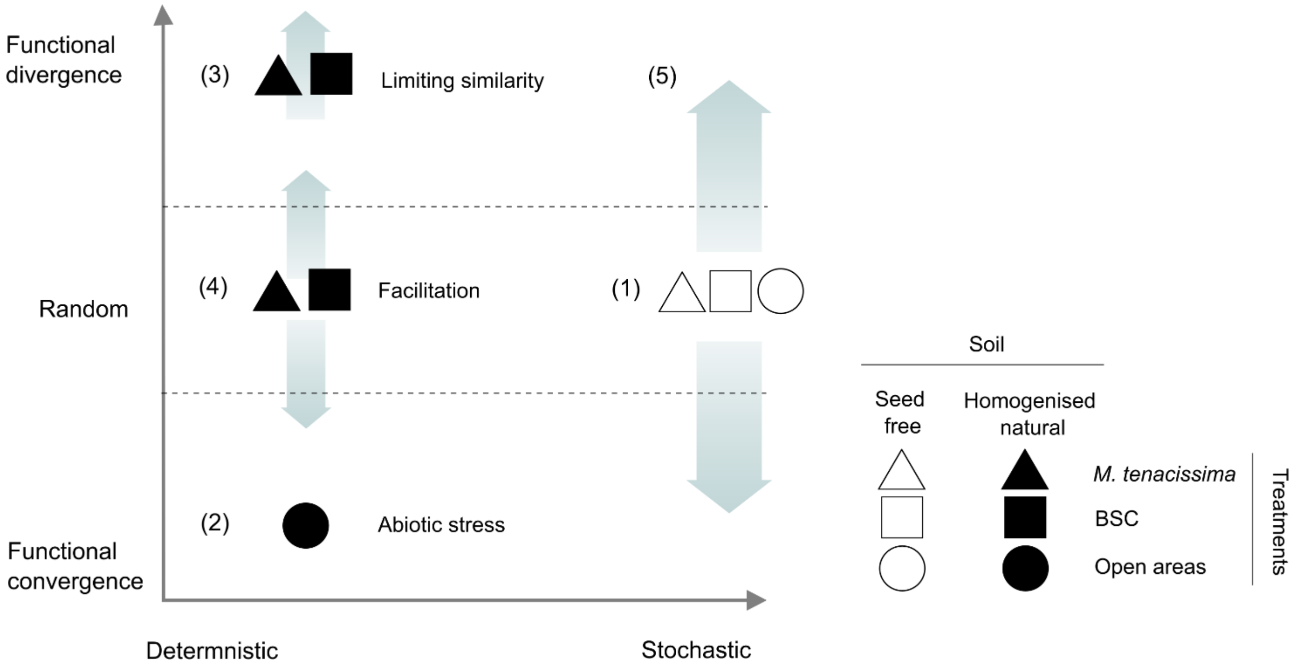

Figure 1. Conceptual framework of the five hypotheses postulated about the participation of stochastic and deterministic processes in plant assembly in dryland gypsum systems: (1) if the contribution of stochastic processes neatly prevails over deterministic environmental filters no functional trait selection would occur, leading to random functional patterns, we expect this will occur in seed free soils; (2) if the presence or absence of biotic components (BSC and *Macrochloa* tussocks) create restrictive microenvironments, it will result in functional convergence in the local species assemblages; (3) if biotic components ameliorate environmental conditions resulting in high biomass production of annual plant assemblages, it would enhance competitive interactions among coexisting species and eventually limiting similarity, leading to functional divergence in the resulting plant communities; (4) if biotic components create milder conditions but not to the extreme of triggering competitive interactions among coexisting species, we may expect stochasticity to prevail; (5) Year to year climate variability may determine shifts in the intensity of abiotic and biotic filtering, if climatic conditions enhance abiotic stress, then functional patterns will move towards functional convergence; on the contrary, if climate conditions increase biomass productivity and enhance intensity of competitive relationships among species then we may expect that functional patterns would shift towards functional divergence in the resulting assemblages; and if climate conditions are in the range of physiological tolerance of species we may expect that stochastic processes will prevail leading to random assemblages.

METHODS

Study site

The study area was a flat summit of 2710 m^2 in a gentle hill zone of a semiarid gypsum steppe located in Sotomayor Experimental Field Station (Aranjuez, central Spain, 40°01′55.7″N - 3°32′48.3″W, 590 m) (Figure 2). The climate is semiarid Mediterranean characterized by the highly variable amount and timing of precipitation among years. Average annual rainfall is 365 mm year^{-1}, concentrated in autumn and spring (142 mm and 96 mm, respectively), and the annual mean temperature is 15°C. Summer period is particularly dry, with mean maximum temperatures achieving 33.2 ºC and mean rainfall of 9 mm in the hottest month (July) (Agencia Estatal de Meteorología, www.aemet.es, Appendix I). The soil is derived from gypsum outcrops and are classified as Gypsiric Leptosols (IUSS Working Group WRB, 2014). Plant community structure on gypsum systems corresponds to that typically described for semiarid areas (Luzuriaga et al., 2012; 2020), formed by plant patches within a matrix of bare soil and well-developed biological soil crusts, having a dense and homogeneously distributed soil seed bank (Peralta et al., 2016; Olano et al., 2012; Caballero et al., 2008a). In our study area, aboveground vegetation is mainly dominated by perennial tussock grasses of *Macrochloa tenaccisima* and some shrubby gypsophile specialists, such as *Helianthemum squamatum* (L.) Dum. Cours., *Lepidium subulatum* L., *Centaurea hyssopifolia* Vahl. and *Gypsophila struthium* L. Seasonally, a very species-rich annual plant community proliferates interspersed among perennial plant patches from October to the end of June. Previous studies in this area registered around 120 annual plant species in the regional species pool (Luzuriaga et al., 2018) and up to 38 species/0.25 m^2 in rainy years (Luzuriaga et al., 2012) (e.g., *Chaenorrhinum reyesii* (C. Vicioso & Pau) Benedí, *Festuca gypsophylla* (Hack.) Paunero, *Campanula fastigiata* Dufour ex Schult, *Alyssum simplex* Rudolphi, *Cerastium glomeratum* Thuill., *Filago pyramidata* L. and *Reseda stricta* Pers.; see Appendix II for a complete list of species found in this study). Squamulose and crustose lichens such as *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (G.H. Weber) Poelt, *Fulgensia subbracteata* (Nyl.) Poelt, *Toninia sedifolia* (Scop.) Timdal, and *Psora decipiens* (Hedw.) Hoffm) dominate BSC along with patches of acrocarpous mosses as *Pleurochaete* *squarrosa* (Brid.) Lindb. and *Tortula revolvens* (Schimp.) G.Roth. (Cano-Díaz et al., 2018; Maestre et al., 2013).

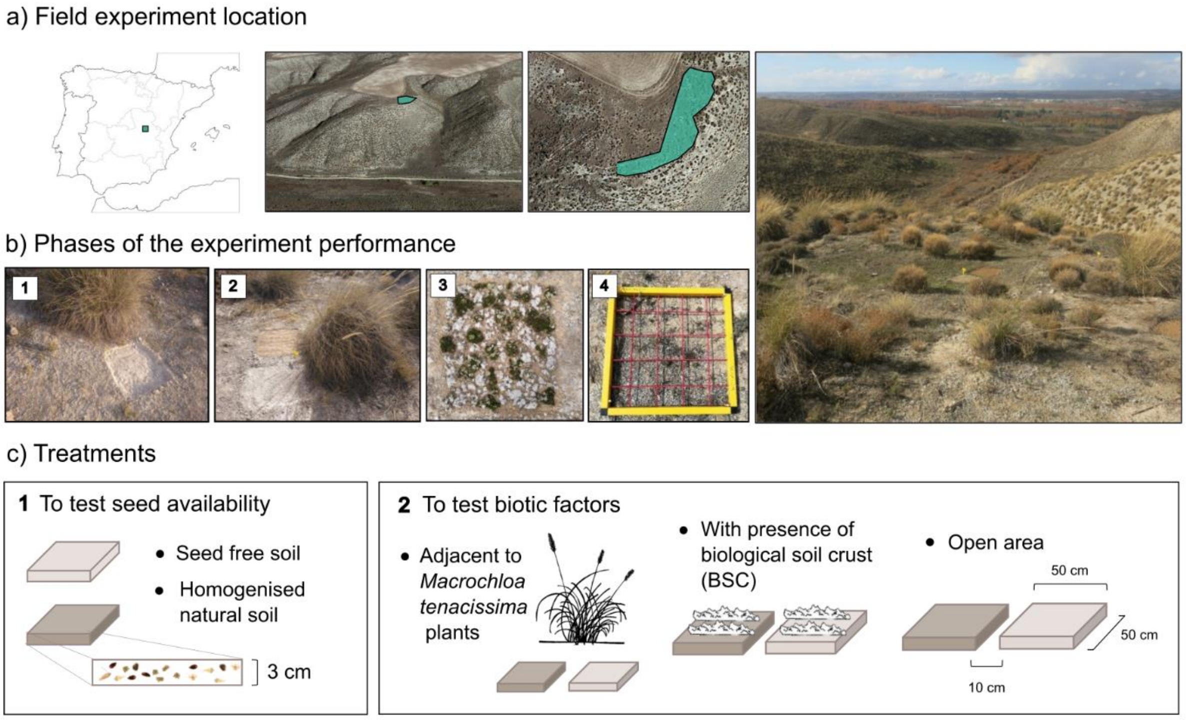

Figure 2. (a) Field experiment location and a general view of the study system. (b) Phases of the experimental performance: (1) excavation of plots; (2) filling of paired plots with homogenized natural soil *vs.* seed free soil from a nearby quarry (seed availability treatment); (3) placing of intact pieces of lichen-dominated biological soil crusts (BSC treatment); (4) detail of plant sampling in a plot, we surveyed the central 30 cm x 30 cm of the sampling frame. (c) Treatments: (1) To test the effects of seed availability (seed free soil *vs*. homogenised natural soil with the complete seed bank) and (2) to test the effects of biotic factors (presence of *Macrochloa tenacissima* tussocks *vs*. presence of biological soil crusts *vs*. open areas).

Experimental design

To assess plant assembly drivers in semiarid gypsum systems, we designed a field experiment that consisted of (i) two treatments to test the effects of seed availability (i.e., soil free of seeds *vs*. homogenised natural soil with the complete seed bank) combined with (ii) three treatments testing the effects of the main biotic components of the system (i.e., presence of BSC *vs*. presence of the perennial *M. tenacissima* tussocks *vs*. open areas) following a complete factorial design with 6 experimental treatments 10-fold replicated (i.e., 60 plots) along four consecutive years (2019 to 2022) (Figure 2).

Seed availability effects were tested by a paired design where two 50 cm x 50 cm square plots were placed in the field parallelly, 10-cm distant, one being filled with seed free soil from a nearby quarry and the other with homogenised natural soil containing a well-structured representation of the seed bank associated to the plant community in this system (homogenised natural soil hereinafter; see Caballero et al. 2008a). To prepare the plots, we dug and removed the 3-cm deep topsoil from the plots in September 2018. In semiarid areas, it is documented that the upper 3-cm soil layer contains most of seeds (Childs & Goodall, 1973). Plot soil extractions were mounded together and thoroughly stirred *in situ*, with a spade, to ensure soil homogenisation. The species-rich soil seed bank of this study system has been shown to be spatially very similar in terms of species composition (Peralta et al 2016; Caballero et al., 2008a), so we can assume that the soil stir operation would assure soil seed bank homogenisation. One plot of each pair was filled with the natural soil containing the homogenised seed bank, and the other plot with seed free soil collected in a gypsum quarry near to the experimental field station (seed availability treatment, hereinafter). Soil moisture level of both seed availability treatments was recorded using a time domain reflectometer (model TDR 100, Campbell Scientific). We found no significant differences in soil moisture among the six treatments (Appendix III).

To test the combined effects of seed availability and biotic factors, we placed 10 plot pairs (i.e., the homogenised natural soil plot along with the corresponding seed free soil paired plots) in each of the three biotic factor levels in the study. For the *M. tenacissima* treatment, we placed a pair of plots in the southern side of each of 10 mature, apparently healthy *M. tenacissima* tussocks. Plots were placed in that orientation because here they receive more insolation and have lower water availability (Pueyo et al., 2007), so the expression of filtering effects mediated by tussocks is expected to be more detectable. Other 10 pairs of plots were placed at least 50 cm away from any perennial plant patch, hereinafter called the open area treatment. The BSC treatment consisted of adding well developed intact pieces of lichen dominated BSC on the soil surface of 10 pairs of plots that were located at least 50 cm away from perennial plant patches. These BSC pieces were carefully collected by using a wide sheet knife, from a similar area adjacent to our study site (Soto de Oreja, 40º01’51’’- 3º29’08’’, 583 m) in September 2018. We tried to select portions of biocrust dominated by *D. diacapsis* and *S. lentigera*, because they predominate in our study area (Luzuriaga et al., 2012; Martínez et al., 2006). Pieces of BSC were extended on plastic drained trays and transported to a greenhouse, where they were subjected to a temperature around 40-50 ºC during the first two weeks to break any possible seed dormancy (see Chaves et al, 2021). After that, BSC was kept at room temperature regularly watered for three months to promote germination of any seed it might have retained. We removed any emergent seedling to ensure BSC free of seeds. In January 2019, we placed the intact pieces of BSC on the surface of the corresponding twenty plots. Biocrust pieces were gently anchored to the plot soil surface by means of a 5-cm light plastic mesh to avoid they were moved out by wind or runoff during early stages of the experiment, when the experimental BSC had not adhered to the soil yet.

Overall, our field experiment was thus performed on 30 pairs of plots (i.e., seed free soil *vs.* homogenised natural soil x *M. tenacissima vs*. BSC *vs*. open areas x 10 replicates) during four consecutive years.

Data collection

The experiment was monitored during four consecutive years, long enough to detect species assembly rules (if manifested) according to previous studies on these dynamic annual-dominated plant communities on gypsum soils (Luzuriaga et al., 2012; 2015). We surveyed plant assemblages in plots during the yearly peak of community development, i.e., April 2019, 2020, 2021, and 2022. In each plot, we identified every species and visually estimated the cover of each one. To do so, we used a 50 cm x 50 cm frame divided into twenty-five 10 cm x 10 cm cells to facilitate counts, and we surveyed the central 30 cm x 30 cm (i.e., we excluded a 10-cm wide plot-edge band) to avoid edge effects. This sample size is enough to capture the dynamics processes of our annual-dominated plant communities (Luzuriaga et al. 2012, 2015).

Climate conditions yearly varied along the experiment, with a widely variable interannual spring-autumn precipitation. The accumulated rainfall amounts from the early rainfall events (September) in the plant life cycle to vegetation maximum development, when sampling was performed (April) were: 109.8 mm/m^2 (2019), 344.6 mm/m^2 (2020), 238.6 mm/m^2 (2021) and 347 mm/m^2 (2022). The historical average rainfall for this period was 289 mm/m^2 (calculated from the 30-year series 1981-2010; Appendix I), thus, we can classify the sampling years as dry (2019), wet (2020 and 2022) and average (2021).

Diversity indexes

For every plot, we calculated species richness, percentage of total plant cover, and the inverse Simpson diversity index based on the relative covers of species, according to the following formula:

$$Inverse\ Simpson\ = \frac{1}{\sum_{i=1}^{S} {p_i}^2}$$

where p_i is the cover proportion of species i and S is the number of species. We used the *diversity* function from the *vegan* package (Oksanen et al., 2020) in R.

We included plant functional traits in our analyses. Information came from the database previously created by Peralta et al. (2019), following the protocols established by Cornelissen et al. (2003) for annual species in the same system of this study. We selected functional traits related to fundamental ecological strategies (Westoby, 1998) linked to plant development and community assembly: (1) specific leaf area (SLA; the ratio of leaf area to leaf dry mass); (2) leaf dry matter content (LDMC; the ratio of leaf dry mass to fresh mass); (3) root:shoot ratio (root/shoot; i.e., belowground:aboveground dry mass ratio); (4) reproductive ratio (rep./veg.; i.e., reproductive:vegetative dry mass ratio); (5) maximum plant height (MPH; i.e., plant stature omitting inflorescences), and (6) seed mass (SM; seed dry weight). Trait information was available for 71.23 % of our species. We used *Rphylopars* (Goolsby et al., 2021) to estimate missing trait values (28.77%) on the basis of the information obtained from the phylogenetic tree (Appendix IV) built using *phylo.maker* function from the *V.PhyloMaker* package (Jin & Qian., 2019) and the *scenario 1* option to bind new tips (see Appendix V for the values of each trait by species). Some traits (root/shoot, rep/veg, MPH and SM) were log transformed prior to statistical analyses to ensure that the data conformed with the assumption of normality.

Community weighted mean (CWM) represents the most probable attribute that an individual would have if drawn at random from a given community (Garnier et al., 2016). Many studies have proven its usefulness in the study of community structure and ecosystem properties (Lavorel et al., 2008; de Bello et al., 2005; Garnier et al., 2004, 2007). We calculated CWM with the following formula:

$$CWM = \sum\nolimits_{i=1}^{N} p_i \, x_i$$

where *N* is the number of species found in each assemblage, p_i is the proportional abundance (based on plant cover) of species *i* in the assemblage (ranging between 0 to 1), and x_i is the trait value of species *i.* We used the *dbFD* function from the *FD* package in R (Laliberté et al., 2014; Laliberté & Legendre, 2010).

Furthermore, we used the standardized mean pairwise dissimilarity index among species (SES.MPD) (Pavoine & Bonsall, 2011) as a functional diversity index. MPD index calculates the mean trait dissimilarity among all possible pairs of species in each assemblage:

$$MPD = \frac{1}{\sum_{i<j}^{N} p_i p_j} \sum_{i<j}^{N} p_i p_j d_{ij}$$

where *N* is the number of species in each assemblage, d_{ij} is the dissimilarity between each pair of different species *i* and *j*, p_i and p_j are the relative abundances of species *i* and *j* (estimated with plant covers) divided by the total of all species abundances in the community (de Bello et al., 2016; Clarke & Warwick, 1998). The standardised mean pairwise dissimilarity index (SES.MPD) is based on the Gower dissimilarities in trait values between all possible pairs of species coexisting in each pot, contrasting the observed MPD with 1000 null models calculated over all subsets of random species:

$$SES.MPD = \frac{MPD_{observed} \; - \; mean\;(MPD_{null)}}{mean\;(MPD_{null)}}$$

So, positive values of SES.MPD mean higher functional divergence, whereas negative values indicate functional convergence in the realized species assemblages. We used the *ses.mpd* function from the *picante* package (Kembel et al., 2010).

Statistical analyses

We conducted a generalized linear mixed model (GLMM) to analyse species richness, and linear mixed models (LMMs) for plant cover and Inverse Simpson of plant assemblages in plots. For all models, seed availability treatment (homogenised natural soil *vs.* seed free soil), biotic factors (*Macrochloa* tussocks, BSC, and open areas), sampling year (2019, 2020, 2021, and 2022), and the interaction between them were considered as fixed factors. Plot identity was included as a random factor. Poisson distribution with log link function were assumed for species richness and Gaussian distribution with identity link function for plant cover and Inverse Simpson.

We built PERMANOVA models to evaluate changes in the compositions of species related to our experimental treatments including biotic factors, seed availability treatment and year as explanatory variables, as well as the interactions between them. We square-root transformed the community composition data to reduce the weighting of dominant species. We used dissimilarity matrices based on the Bray–Curtis distance (Anderson, 2007) and type III sums of squares. Plot identity was included as a strata factor. We performed non-metric multidimensional scaling (NMDS) to visualize the differences in the species composition among the three biotic factors and for each seed availability treatment for each year.

We performed LMMs to explain variations in CWM and SES.MPD values for each trait (SLA, LDMC, root/shoot, rep/veg, MPH and SM). We considered seed availability treatment (homogenised natural soil *vs.* seed free soil), biotic factors (*Macrochloa* tussocks, BSC, and open areas), sampling year (2019, 2020, 2021, and 2022), and the interaction between them as fixed factors. Plot identity was included as a random factor to consider the repeated measures during the four study years. We assumed Gaussian distribution with identity link function for all models.

We used the *glmer and lmer* functions from the *lme4* package (Bates et al., 2015) to perform GLMMs and LMMs analyses, respectively. We used the *adonis* function to perform PERMANOVA models and metaMDS function to perform NMDS' from the *vegan* package (Oksanen et al., 2020). We performed Tukey HSD post-hoc test with *emmeans* function from the *emmeans* package (Russell, 2022). All analyses were carried out with the R software version 4.0.5 (R Core Team, 2021).

RESULTS

Species richness, plant cover, and taxonomic diversity

During the four study years, we registered 73 species of 26 families: 67 annuals and six perennials (Appendix II). Realized assemblages were highly variable in species richness at the fine spatial scale (ranging between 1 and 21 species/0.09 m^2). Total species richness comprised in all the study plots varied among years, being 38, 51, 47, and 36 in 2019, 2020, 2021, and 2022, respectively, as well as mean richness per plot between years (3.83 in 2019, 7.07 in 2020, 6.63 in 2021 and 6.53 in 2022). Mean plant cover per plot ranged from 2.3% in the first year, to 7.1% in the second, 14.2% in the third year, and 9% in the fourth year. Mean taxonomic diversity per plot (inverse Simpson index) was 1.68, 2.9, 2.57, and 2.4 in 2019, 2020, 2021, and 2022, respectively.

Soil seed availability, biotic treatments and year explained variability in taxonomic properties and total cover of the resulting assemblages (Table 1). In general, assemblages were more complex (i.e., species richness and taxonomic diversity) and productive (i.e., plant cover) in plots that originated from homogenised natural soils than from seed free soils, except in the BSC treatment (Figure 3). Indeed, BSC promoted higher species richness, plant cover, and diversity in both seed availability treatments, which closely equalled their richness and taxonomic diversity values from the second year (Figure 3a and c). In open areas, assemblages had higher species richness, diversity, and total cover in homogenised natural soil than in seed free plots; these differences tended to disappear with years (Figure 3). Next to *M. tenacissima* tussocks, the expression of plant communities was restricted, as revealed by the generally low taxonomic diversity values, and especially low total plant cover, which was even lower than in open areas (Figure 3b). All these assemblage responses to the biotic microenvironments were, in addition, modulated by the year (Table 1 and Figure 3). As expected, taxonomic properties of the species assemblages varied along the four study years.

Table 1. Generalized linear mixed model (GLMM) to analyse species richness, and Linear Mixed models (LMMs) to analyse total plant cover, and Inverse Simpson in experimental assemblages (n = 239). Biotic treatment (B; open areas, biological soil crusts, *Macrochloa tenacissima*), seed availability treatment (SA; seed free soil, homogenised natural soil) and study year (Y; 2019, 2020, 2021, 2022) were included in the model as fixed factors, and plot identity as a random factor. Family distribution and link that best suited our models are indicated. Type III Wald Chi-square tests are indicated. Significant results are shown in bold, and significance is indicated with asterisks: ***p<0.001; **p<0.01; *p<0.05; †p<0.1. Df: degrees of freedom.

		Richness	**Cover**	**Inverse Simpson**
	Error distr. Link	Poisson log	Gaussian identity	Gaussian identity
	Df	Chisq	Chisq	Chisq
Intercept	1	233.4	5.8	49.1
Biotic treatment (B)	2	**20.6 *****	2.5	5.1 †
Seed availability (SA)	1	**41.6 *****	2.6	**13.1 *****
Year (Y)	3	7.8 †	**35.6 *****	4.2
B:SA	2	**7.9 ***	1.2	2.6
B:Y	4	**34.6 *****	**46.4 *****	**16.3 ***
SA:Y	2	**16.8 *****	**14.1 ****	6.7 †
B:SA:Y	4	6.9	7.2	3.1

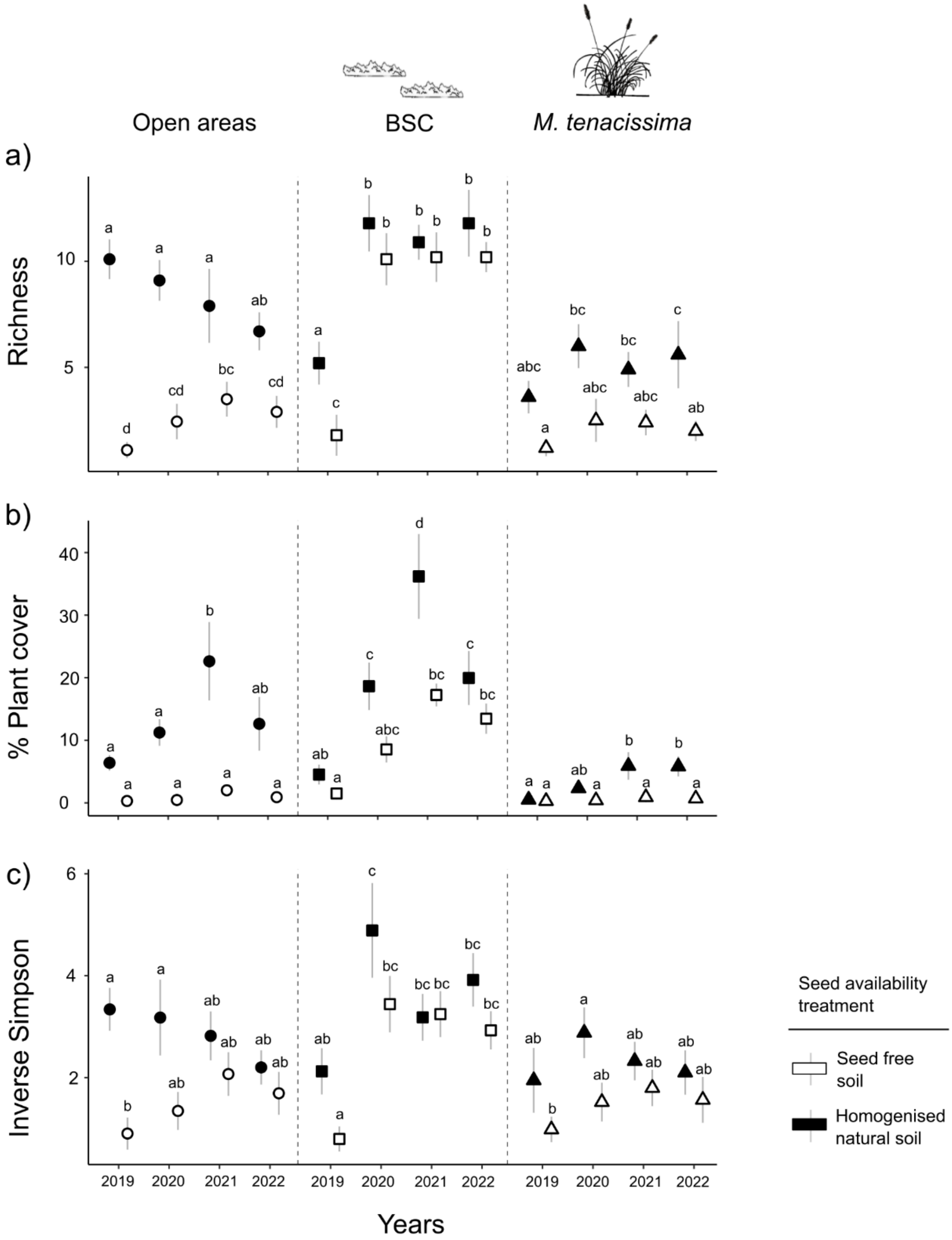

Figure 3. Representation of mean values (± standard error) of species richness (a), percentage of total plant cover (b) and Inverse Simpson (c) in assemblages. For each biotic treatment (open area, biological soil crust, and *Macrochloa tenacissima*) and community feature, different letters represent significant differences among seed availability treatments and years (eight different scenarios) tested with estimated marginal means.

Interannual variability, biotic treatments and seed availability also determined the species composition of assemblages. Our model overall explained 27% of the variance in species composition (Table 2). Differences in species composition among treatments (both seed availability and biotic components) occurred mainly in the first year (2019; Figure 4). Species composition became more similar between both seed availability treatments with time throughout the study (Figure 4a). Remarkedly, in the last sampling year (2022), assemblages developed in the BSC treatment and in open areas had similar species compositions, while species composition next to *M. tenacissima* tussocks kept visible differences (Figure 4b).

Table 2. Results of PERMANOVA analysis to model the effect of biotic factors (B; open area, biological soil crusts, *Macrochloa tenacissima*), seed availability treatment (SA; seed free soil, homogenised natural soil) and study years (Y; 2019, 2020, 2021, 2022) and their interaction terms on species composition (n=215). Plot identity was included as a strata to control for repeated measures in the four study years. Original data was square root-transformed. Bray–Curtis dissimilarities and Type III sum of squares were used. Df: degrees of freedom; F:F-ratio; R2: proportion of variation explained.

	Df	F	R^2	p
Biotic treatment (B)	2	7.1	0.05	**0.0001**
Year (Y)	3	7.6	0.08	**0.0001**
Seed availability (SA)	1	8.5	0.03	**0.0001**
B:Y	6	1.8	0.04	**0.0001**
B:SA	2	2.9	0.02	**0.0001**
Y:SA	3	2.7	0.03	**0.0001**
B:Y:SA	6	0.8	0.02	0.504
Residuals	192		0.7	
Total	215		1.0	

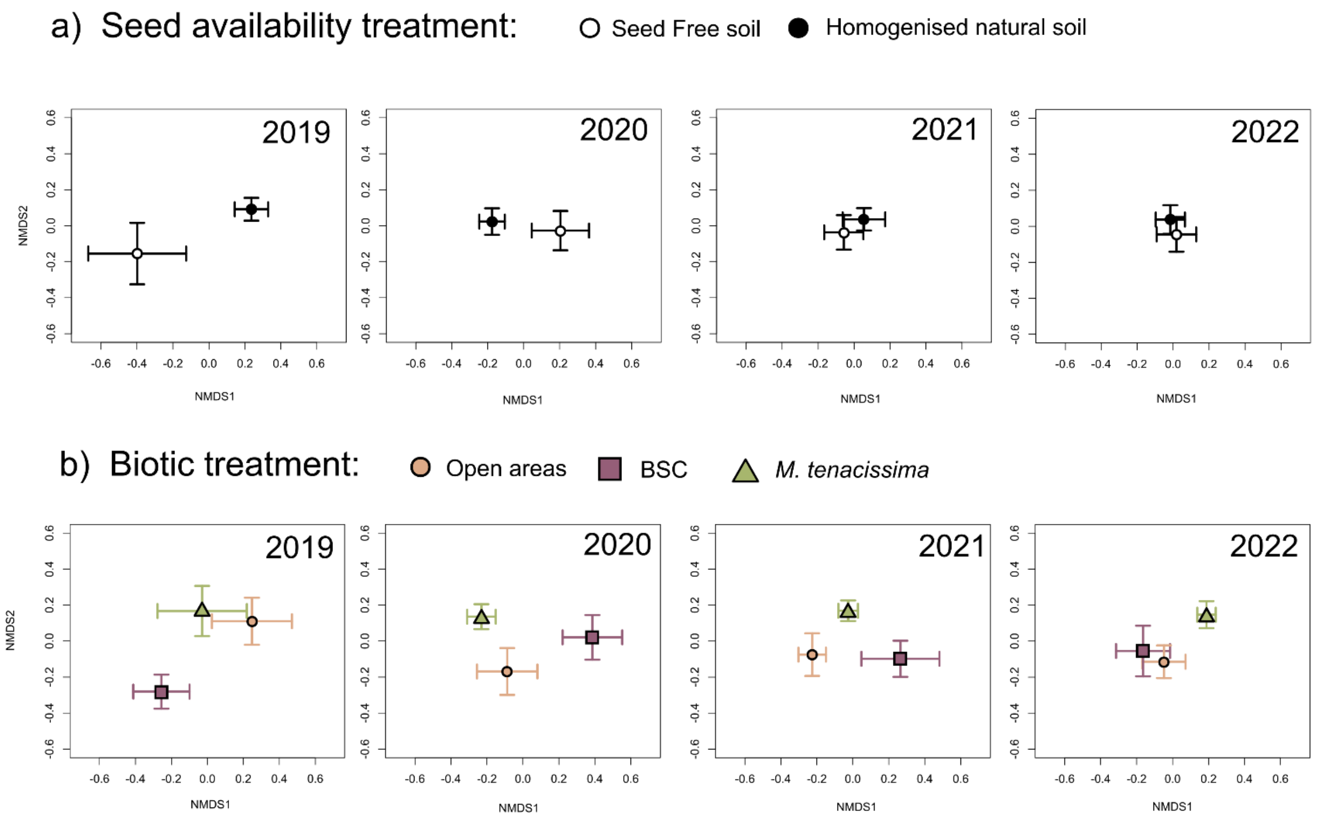

Figure 4. Non-metric multidimensional scaling (NMDS) ordination; based on the species compositions in plots. Centroids and error bars for the biotic (open area, biological soil crust, *Macrochloa tenacissima*) and seed availability (seed free soil, homogenised natural soil) treatments are shown. Differences between seed availability treatments over study years are shown in the top panels (a), and differences among biotic treatments over study years are shown in the bottom panels (b). In terms of rainfall amount, years were classified as dry (2019), wet (2020, 2022), and average (2021).

Functional diversity

Interannual variability was the main source of differences in the functional structure of assemblages (Table 3). Early assemblages in our study (2019) showed high SLA$_{CWM}$ (Figure 5a-d), rep/veg$_{CWM}$ (Figure 5c) and LDMC$_{CWM}$ (Figure 5d), which decreased over time. The opposite temporal trend was recorded for root/shoot$_{CWM}$. This means that species with high SLA, rep/veg and LDMC values were dominant in early species assemblages and in subsequent years other species with lower values for these traits proliferated. contrarily occurred for the values of Root/shoot ratio of species along the four study years. Biotic treatments in combination with year was significant for LDMC$_{CWM}$ and MPH$_{CWM}$ (Table 3a). Maximum stature (MPH) of species assembling in BSC and *M. tenacissima* plots tended to decrease with time, while no temporal change was recorded for this trait in open areas (Figure 5e). This means that the species that established near *M. tenacissima* and with BSCs have larger maximum plant sizes in early species assemblages and along the study years other species with smaller maximum statures entered the communities. We observed a decrease in LDMC$_{CWM}$ values in assemblages developed in open areas over the years (Figure 5f), Thus, species with lower LDMC values became dominant in species assemblages of open areas along the four study years.

We observed a clear difference in SLA$_{SES.MPD}$ values between the second year (2020) and the third year (2021) (Figure 6a) but no differences were observed for the first and last years (2019 and 2022). For LDMC$_{SES.MPD}$ values, we observed an increasing along study years, with the highest value in the third year (Figure 6b). Biotic treatments in combination with year was significant for MPH$_{SES.MPD}$ (Table 3b, Figure 6c). Early assemblages showed very similar values but from the second year onwards we observed a reduction in the values in presence of BSC. In presence of *M. tenacissima,* the tendency was to increase in the second and third years. In the case of open areas, there was no clear trend (Figure 6c).

Table 3. Results of Linear mixed models (LMMs) to evaluate the effect of the experimental scenarios on a) community weighted mean (CWM), and b) standardized mean pairwise distance index (SES.MPD) values for plant traits. Year (Y; 2019, 2020, 2021, 2022), biotic treatments (B; open areas, biological soil crusts, *Macrochloa tenacissima*), soil availability treatment (SA; seed free soil, homogenised natural soil), and their interactions, were included in the models as fixed effects, and plot identity as a random factor. Traits evaluated: specific leaf area (SLA)(mm^2/mg); leaf dry matter content (LDMC)(mg/g); root:shoot ratio (root/shoot; i.e., belowground:aboveground dry mass ratio); reproductive ratio (rep./veg.; i.e., reproductive:vegetative dry mass ratio); maximum plant height (MPH; i.e., plant stature omitting inflorescences) (mm) and seed mass (SM)(µg). We used Gaussian distributions with identity link functions. Significant values are shown in bold, and significance indicated with asterisks: ***p<0.001; **p<0.01; *p<0.05; †p<0.1. DF: defrees of freedom.

a) CWM

		SLA (mm^2/mg)	LDMC (mg/g)	Root/shoot	Rep/veg	MPH (mm)	Seed mass (µg)
	Df	Chisq	Chisq	Chisq	Chisq	Chisq	Chisq
(Intercept)	1	117.5 ***	295.3 ***	309.7 ***	10.8 ***	440.7 ***	119.9 ***
Year (Y)	3	**12.8** **	**22.0** ***	**16.9** ***	**12.5** **	4.7	5.8
Seed availability (SA)	1	0.1	1.1	0.4	0.0	0.3	0.3
Biotic treatment (B)	2	0.0	0.3	0.5	1.0	0.8	0.5
Y:SA	3	6.2	6.3 †	4.0	6.8 †	3.2	3.5
Y:B	6	4.9	**13.6** *	8.2	12.1 †	**15.6** *	10.3
SA:B	2	0.8	0.6	0.2	0.3	1.9	0.3
Y:SA:B	6	4.3	4.1	3.9	8.8	7.2	6.5

b) SES.MPD

		SLA (mm^2/mg)	LDMC (mg/g)	Root/shoot	Rep/veg	MPH (mm)	Seed mass (µg)
	Df	Chisq	Chisq	Chisq	Chisq	Chisq	Chisq
(Intercept)	1	0.1	7.2 ***	2.0	0.2	0.9	2.0
Year (Y)	3	**10.7** *	**18.2** **	3.7	1.0	5.7	6.1
Seed availability (SA)	1	0.5	0.0	0.0	0.0	0.8	1.1
Biotic treatment (B)	2	1.0	1.2	0.2	0.5	0.7	0.6
Y:SA	3	5.5	2.5	0.8	1.9	2.5	1.5
Y:B	6	7.4	4.8	9.1	2.8	**12.7** *	4.6
SA:B	2	0.6	0.1	2.0	0.3	5.6 †	2.1
Y:SA:B	6	2.6	3.9	1.7	2.9	10.1	2.6

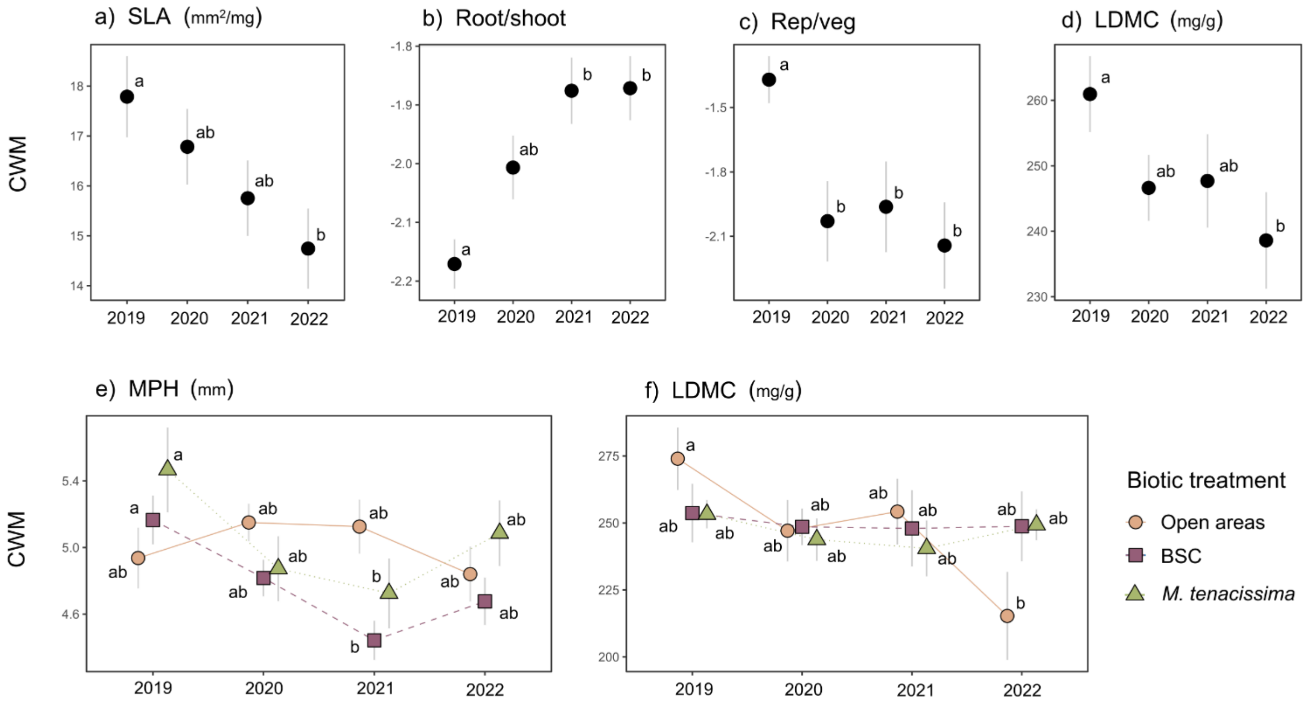

Figure 5. Mean values for community weighted means (CWM) for the significant terms shown in Table 3a. Vertical bars represent standard errors. Different letters represent significant differences among treatments and /or years tested with estimated marginal means.

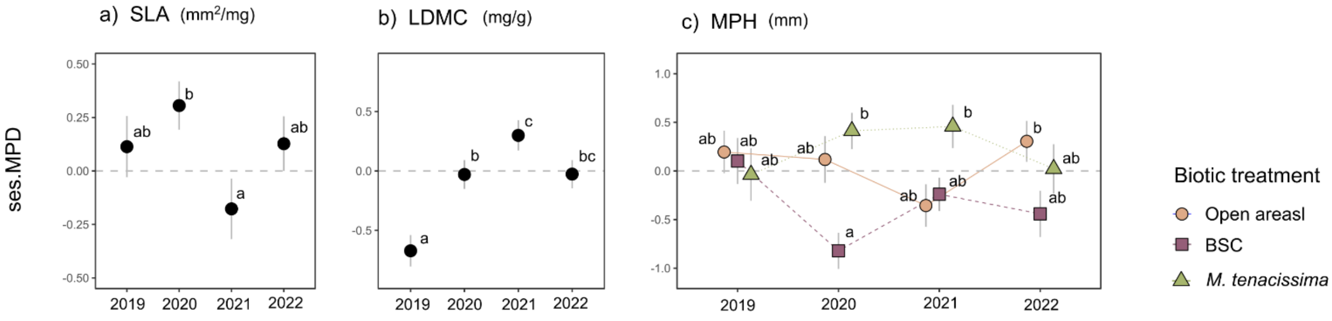

Figure 6. Mean values for standardized mean pairwise distance functional index (SES.MPD) for the significant terms shown in Table 3b. Different letters represent significant differences among treatments and/or years tested with estimated marginal means.

DISCUSSION

Our 4-year field experiment reveals that stochastic processes were dominant in the generation of assemblages, especially in years with average or above average rainfall. In contrast, functional trait selection associated to biotic environmental filters were anecdotal. In addition, it is worth noting the role played by the presence of BSC, increasing richness, total cover, and taxonomic diversity, that equalized species assemblages in seed free and homogenised soil conditions. Surprisingly, our results are in line with other studies that evaluated species assembly processes in highly favourable environments, where species tend to assemble stochastically (Chase & Myers, 2011).

Our results related to the effects of water availability are in line with previous studies in gypsum semiarid systems (Sánchez et al., 2022; Peralta et al., 2019) that manipulated the availability of water in these communities, in which the importance of timing and amount of precipitation in the formation of annual plant communities was already demonstrated. They only detected trait selection when water stress was very strong, specifically, when the irrigation treatment reduced the water amount to one third of the average rainfall in the study area. The availability of water is a crucial factor in the formation of annual-dominated communities (Huxman et al., 2013; Levine et al., 2011). Concretely, in semi-arid gypsum systems, timing and amount of rainfall is modulated by the high inter-annual variability of annual rainfall (Vargas-Colin et al., 2022; Luzuriaga et al., 2012, 2015). Even although drought events are relatively frequent in our system, during our 4-years experiment we experienced only one year with below-average precipitation values (i.e., 2019), while for the rest, precipitations were higher or equal to the average (see Appendix I). Our communities seem to be adapted to this climatic variability (Tielbörger et al., 2014) and in years when conditions are more favourable, they take advantage of this to establish. Moreover, these communities are very resilient and a single year with high water availability allows taxonomic and functional recovery of species assemblages after several dry years (see López-Rubio et al., 2022). Therefore, climatic inter-annual variability plays a key role inducing alternative assembly scenarios with different functional combinations (Violle et al., 2017).

We observed that stochastic processes were conspicuous in both seed availability treatments (seed free soil and homogenised natural soil). In these systems, there is a large horizontal movement of seeds widely documented (Martínez-Duro et al., 2009, 2010): the low vegetation cover together with the active wind and runoff processes may promote a very active secondary dispersal. It should be noted that, despite active secondary seed dispersal in the system, the assemblages in the unseeded soils and in the homogenised natural soil treatments did not equalise, in terms of taxonomy and cover, as quickly as might be expected. In fact, in the fourth year there were still significant differences in species richness between the two seed availability treatments. We may expect that semiarid systems are really harsh habitats where deterministic processes would prevail, however, our results evidenced that stochastic processes were dominant in this system. Our species, that have evolved in these dryland gypsum environments over thousands of years, may therefore have drought tolerance thresholds well above the water stressful conditions occurred during the four concrete study years. During most of our study, the rainfall amount was average or even above average. Therefore, most likely within the tolerance ranges of our species, these years have been very favourable for our species pool and in that sense, they behaved like species with no significant water restrictions (Hubbell, 2006; Harms et al., 2001; Webb & Peart, 2000; Pitman et al., 1999), meaning that when there was an opportunity, they established but there has been no directional selection. Our results are further evidence of the need to take into account both niche theory and neutral theory, as many previous studies supported (Qiao et al., 2015; Weiher et al., 2011; Vellend, 2010; Vergnon et al., 2009; Alonso et al., 2006; Holt, 2006; Pacala & Tilman, 1994). Specifically, in our study system, although species have niche and functional trait differentiation, such differences may be of minor importance for species assembly processes in years with average precipitation and wet years (Holt, 2006), and probably the relative importance of neutral processes may decrease with increasing environmental stress (Qiao et al., 2015). To completely confirm this, we would need to extend our field experiment to years with more marked environmental stress, such as severe drought.

Notably, the presence of BSC had significant effects on our annual dominated communities. Thus, the movement and the consequent arrival of seeds was clearly manifested in our assemblages with presence of BSC, where, just one year after the experiment setup, taxonomic richness, diversity, and species composition on homogenised natural and seed free soils were equalised. This could be explained because the structure created in the soil by the presence of BSC profusely trapped seeds in their horizontal movement (stochastic process) (Bowker et al., 2018; Zhang et al., 2016), which in combination with the amelioration of microenvironmental conditions under their influence (Boeken, 2008; Belnap, 2003) may enhance fast recovery of soil seed banks and species assemblages. Thus, in our system BSC seems to act as a powerful seed-trapping agent (Bowker et al., 2018; Zhang et al., 2016) that retained them and provided ameliorated conditions (Belnap et al., 2016) to the survival and growth of the seedlings once they emerged (Ortiz et al., 2023). Even to the extent of compensating for the initial absence of seeds in the soil. It is therefore important to emphasise the conservation (non-disturbance) of the BSC. In the other scenarios, such as open areas, it is possible that seeds may have kept on moving on the soil surface in the absence of structures that favoured seed retention. It may be necessary to wait for the BSC reconstruction for the plant assemblages to become fully established there.

Contrary to our expectations, in the presence of *M. tenacissima* perennial tussocks we did not observe this seed-trapping effect (Bullock & Moy, 2004), because plots with and without presence of *M. tenacissima* did not equalise in terms of richness and cover, furthermore the two seed availability treatments remained different, until the last year of the study. In open areas, we also found no equalisation of species richness between both soil treatments in the four study years. On the other hand, contrary to what we expected from previous studies (Pugnaire et al., 2011; Maestre et al., 2007) the presence of *Macrochloa* plants did not have a clear facilitating effect. Although previous studies point to the idea that perennial plants act as nurse plants and exert facilitating effects in arid ecosystems (Madrigal-González et al., 2020; Luzuriaga et al., 2012; Maestre et al., 2007; 2001), our results showed a different scenario. One possible explanation could be that the water consumed by *Macrochloa* tussocks is greater than the amount of water collected in the surrounding soil area, thus creating a direct competition for water between annual-dominated community and *M. tenacissima* plants (Maestre et al., 2003).

We observed an equalizing temporal trend in taxonomic composition of the assemblages developed in contrasting experimental scenarios along the four study years: clearly between the two soil types, and, although with a less clear temporal pattern, between microenvironments, particularly BSC and open areas. It should be noted that the open areas and the areas with a BSC presence have very similar species compositions by the fourth year. This could be explained by the fact that, from the fourth year onwards, well-developed BSC started to appear in the open areas. This would contrast with previous studies (Kidron et al., 2020) that described the recovery of BSC from propagules in the soil as a much slower process than we have witnessed in the field. The BSC that started to establish in the homogenised soil scenarios in open areas is probably not as diverse as a well-preserved BSC, but it definitely exerted a similar role for annual species establishment. On the other hand, in the areas adjacent to *M. tenacissima*, assemblages kept more distant in terms of species composition during the whole study, probably because *M. tenacissima* may have competed with assemblages, restricting their expression, and even with the BSC, hindering the development of a well-structured BSC nearby them.

In our study, we did not detect any filtering of functional traits associated with specific microenvironments, that means, deterministic filtering does not seem to play a prominent role, at least in these early stages of recovery of the assemblages. However, the identification of the dominant functional traits of the species assemblages conformed along the four study years allowed us to understand the replacement of the dominant characteristics of the species that establish along community development starting from homogenised and seed free soils. Specifically, our results showed that pioneer species showed high SLA, Rep/Veg and LDMC values and low root/shoot values, while the following years more conservative species dominated species assemblages showing lower values in the three former traits and higher values in the latter, following a typical progression of succession. We refer to pioneer species as species with very productive leaves and low root investment. According to niche complementarity and limiting similarity (MacArthur & Levins, 1967) theories, species arriving at a new site are more likely to become established when their functional traits allow them to occupy an empty niche in the community (Galland et al., 2019; Thuiller et al., 2009).

To conclude, our results confirm that the arrival of propagules (stochastic process) has a special relevance in the assembly of gypsum annual-dominated plant communities. It seems that seeds move actively across the soil surface and established wherever they had the opportunity, homogenising the assemblages in taxonomic terms, without a clear selection of traits and species by any of the factors studied, as we postulated in Hypothesis 1 (see Figure 1). The biotic components (presence of *Macrochloa tenacissima* and BSC) influenced community formation, for example, presence of BSC resulted in higher species richness and plant cover, and presence of *M. tenacissima* modified species composition. Contrarily to our expectations, biotic components did not exert functional convergence of the coexisting species (Hypothesis 2) neither did they enhance biotic interactions among annual plants to promote functional divergence (Hypothesis 3). Our results agree with Hypothesis 4, that postulates that if biotic components did not have restrictive effects neither did they promote competitive interactions among coexisting species, we may expect stochasticity to prevail in the resulting assemblages. In fact, this study is the first evidence that shows that in semiarid systems, stochasticity could be the main driver of assembly processes. We suggest that in our case, the average or even above average rainfall values of the study years, may be favourable enough for the species in the regional pool to establish and complete their life cycles, since these species have evolved to cope with even more restrictive conditions, and consequently, stochastic processes prevailed leading to random assemblages (Hypothesis 5). With this study we have contributed to provide information on one of the most important topics of community ecology, which is to determine and understand the rules governing the assemblage processes (Cavender-Bares et al., 2009; Weiher & Keddy, 1999) and also we shed light on the role of seed dispersal and microhabitat in the assembly of communities (Valiente-Banuet & Verdú, 2007; Callaway 1995).

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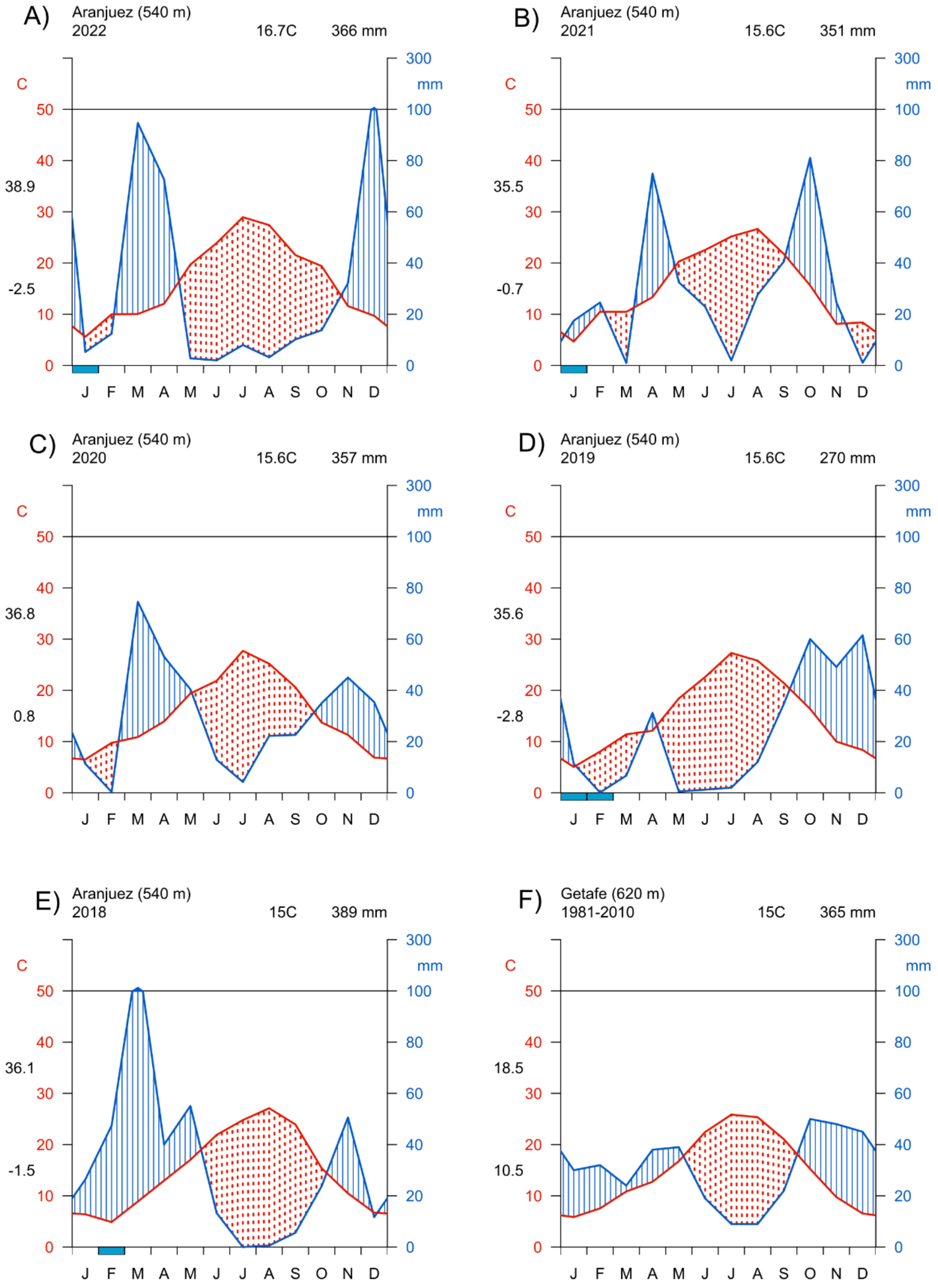
Supporting information

CHAPTER 1

Assessing the contribution of deterministic vs. stochastic processes to local species assembly: a field experiment with annual-dominated plant communities in gypsum systems

Laura Ortiz, Arantzazu L. Luzuriaga, Lars Götzenberger and Pablo Ferrandis

Appendix I. Climographs for the study site in Aranjuez (Madrid, Spain) for the years: A) 2022, B) 2021, C) 2020, D) 2019 and E) 2018. Graphic F) represents the average climograph for the 30-year 1981-2010 series in the nearest long-term weather station from the study site (Getafe, Madrid).

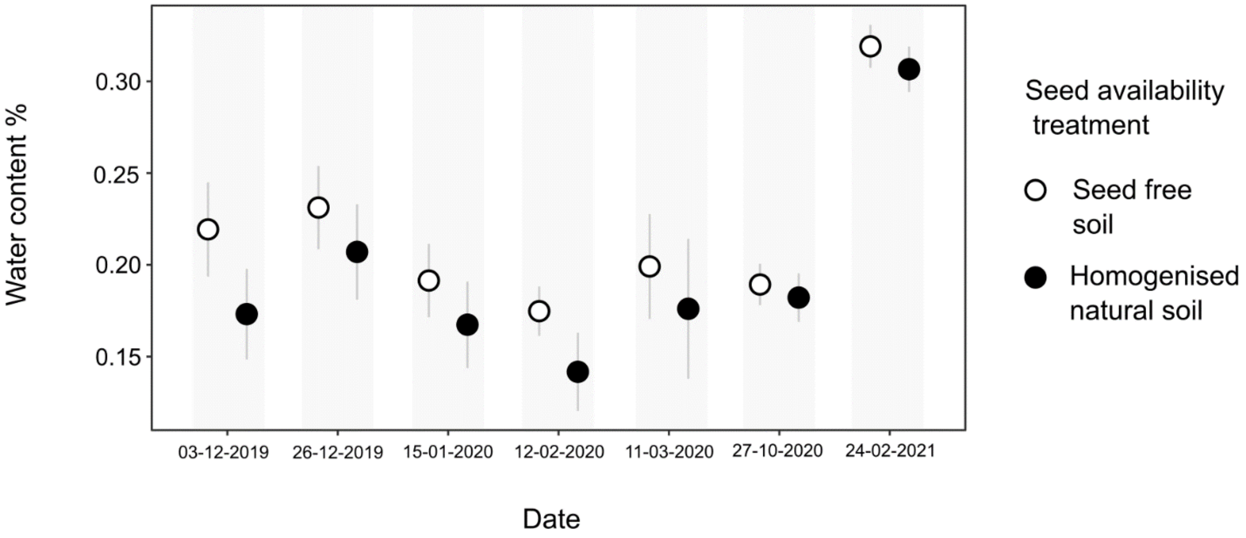


Appendix II. Plant species recorded in the study area along the four study years. Botanic family and life cycle are indicated for each one.

Species	Family	Life cycle
Allium sphaerocephalon L.	Amaryllidaceae	Perennial
Alyssum simplex Rudolphi	Brassicaceae	Annual
Anagallis arvensis L.	Primulaceae	Annual
Anchusa azurea Mill.	Boraginaceae	Annual
Asteriscus aquaticus (L.) Less.	Asteraceae	Annual
Asterolinon linum-stellatum (L.) Duby in DC	Primulaceae	Annual
Astragalus stella L.	Fabaceae	Annual
Bartsia trixago L.	Orobanchaceae	Annual
Bombycilaena discolor (Pers.) Laínz	Asteraceae	Annual
Brachypodium phoenicoides (L.) Roem. & Schult.	Poaceae	Annual
Bromus rubens L.	Poaceae	Annual
Campanula erinus L.	Campanulaceae	Annual
Campanula fastigiata Dufour ex A.DC.	Campanulaceae	Annual
Centaurea hyssopifolia Vahl.	Asteraceae	Annual
Centaurea melitensis L.	Asteraceae	Annual
Centaurium quadrifolium (L.) G. López & C.E. Jarvis	Gentianaceae	Annual
Centranthus calcitrapae (L.) Dufr.	Caprifoliaceae	Annual
Cerastium glomeratum Thuill.	Caryophyllaceae	Annual
Chaenorhinum reyesii (C. Vicioso & Pau) Benedí	Plantaginaceae	Annual
Cirsium sp.	Asteraceae	Annual
Dipcadi serotinum (L.) Medik	Asparagaceae	Annual
Diplotaxis sp.	Brassicaceae	Annual
Echium vulgare L.	Boraginaceae	Annual
Erodium botrys (Cav.) Bertol.	Geraniaceae	Annual
Erodium cicutarium (L.) L'Her	Geraniaceae	Annual
Erodium pulverulentum (Cav.) Willd	Geraniaceae	Annual
Eruca vesicaria (L.) Cav.	Brassicaceae	Annual
Euphorbia falcata L.	Euphorbiaceae	Annual
Euphorbia sulcata Lens ex Loisel.	Euphorbiaceae	Annual
Filago pyramidata L.	Asteraceae	Annual
Frankenia sp.	Frankeniaceae	Annual
Galium parisiense L.	Rubiaceae	Annual
Hedypnois cretica (L.) Dum.	Asteraceae	Annual
Helianthemum salicifolium (L.) Mill.	Cistaceae	Annual
Helianthemum squamatum (L.) Dum. Cours.	Cistaceae	Perennial
Herniaria cinerea DC. in Lam. & DC.	Caryophyllaceae	Annual
Hippocrepis ciliata Willd.	Fabaceae	Annual
Holosteum umbellatum L.	Caryophyllaceae	Annual
Hornungia petraea (L.) Rchb.	Brassicaceae	Annual

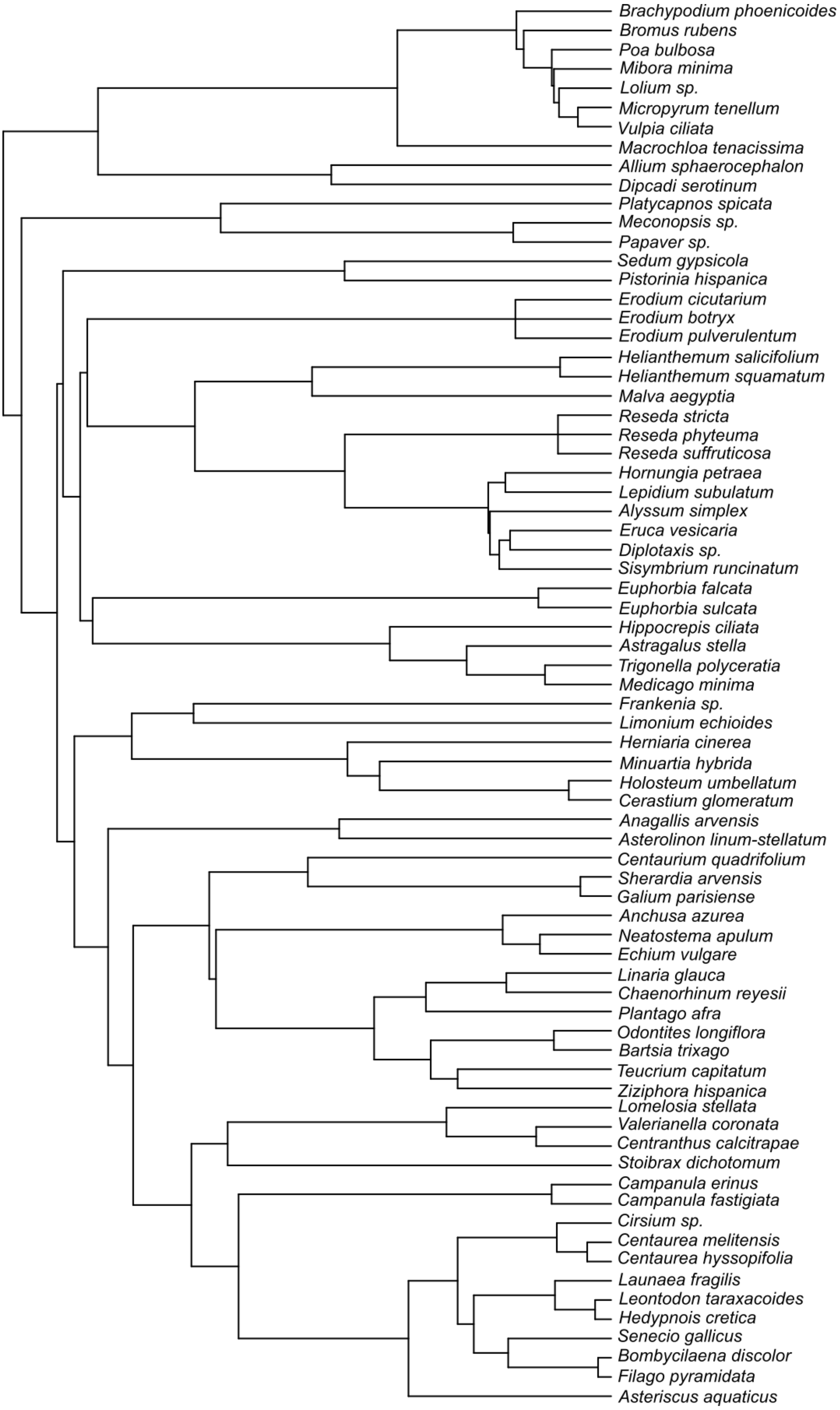
Launaea fragilis (Asso) Pau.	Asteraceae	Perennial
Leontodon taraxacoides (Vill.) Mérat.	Asteraceae	Annual
Lepidium subulatum L.	Brassicaceae	Perennial
Limonium echioides (L.) Miller	Plumbaginaceae	Annual
Linaria glauca (L.) Chaz.	Plantaginaceae	Annual
Lomelosia stellata (L.) Raf.	Caprifoliaceae	Annual
Macrochloa tenacissima (L.) Kunth	Poaceae	Perennial
Macrosyringion longiflorum (Vahl) Rothm.	Orobanchaceae	Annual
Malva aegyptia L.	Malvaceae	Annual
Meconopsis sp.	Papaveraceae	Annual
Medicago minima (L.) L.	Fabaceae	Annual
Mibora minima (L.) Desv.	Poaceae	Annual
Micropyrum tenellum (L.) Link.	Poaceae	Annual
Minuartia hybrida (Vill.) Schischk.	Caryophyllaceae	Annual
Neatostema apulum (L.) I.M.Johnst	Boraginaceae	Annual
Odontites longiflora (Vahl) Webb	Orobanchaceaea	Annual
Papaver sp.	Papaveraceae	Annual
Pistorinia hispanica (L.) DC.	Crassulaceae	Annual
Plantago afra L.	Plantaginaceae	Annual
Platycapnos spicata (L.) Bernh.	Papaveraceae	Annual
Poa bulbosa L.	Poaceae	Annual
Reseda phyteuma L.	Resedaceae	Annual
Reseda stricta Pers.	Resedaceae	Annual
Reseda suffruticosa Loefl. ex Koelp.	Resedaceae	Annual
Sedum gypsicola Boiss. & Reut.	Crassulaceae	Perennial
Senecio gallicus Vill.	Asteraceae	Annual
Sherardia arvensis L.	Rubiaceae	Annual
Sisymbrium runcinatum Lag. ex DC.	Brassicaceae	Annual
Stoibrax dichotomum (L.) Raf.	Apiaceae	Annual
Teucrium capitatum L.	Lamiaceae	Annual
Trigonella polyceratia L.	Fabaceae	Annual
Valerianella coronata (L.) DC.	Caprifoliaceae	Annual
Vulpia ciliata Dumort.	Poaceae	Annual
Ziziphora hispanica L.	Lamiaceae	Annual

Appendix III. Mean values of the soil water content (%) in plots with different seed availability treatments (seed free soil and homogenised natural soil) recorded during the experiment, measured by using a time domain reflectometry (TDR) method. Vertical bars represent standard errors. The table below shows the results of the Tukey test for significant differences between treatments.



Date	Groups	estimate	conf.low	conf.high	p.adj	p.adj.signif
03/12/2019	Free seed soil- Homogenised natural soil	-0.046	-0.126	0.033	0.224	ns
26/12/2019	Free seed soil- Homogenised natural soil	-0.024	-0.101	0.053	0.500	ns
15/01/2020	Free seed soil- Homogenised natural soil	-0.024	-0.093	0.045	0.454	ns
12/02/2020	Free seed soil- Homogenised natural soil	-0.033	-0.089	0.023	0.219	ns
11/03/2020	Free seed soil- Homogenised natural soil	-0.023	-0.129	0.083	0.639	ns
27/10/2020	Free seed soil- Homogenised natural soil	-0.007	-0.046	0.032	0.691	ns
24/02/2021	Free seed soil- Homogenised natural soil	-0.012	-0.051	0.026	0.483	ns

Appendix IV. Distance based phylogenetic tree for the 73 species recorded along the three study years. Based on V.PhyloMaker package in R.



Appendix V. Values of functional traits for plant species recorded in the study area. (1) specific leaf area (SLA)(mm^2/mg); (2) leaf dry matter content (LDMC)(mg/g); (3) root:shoot ratio (root/shoot; i.e., belowground:aboveground dry mass ratio); (4) reproductive ratio (rep./veg.; i.e., reproductive:vegetative dry mass ratio); (5) maximum plant height (MPH; i.e., plant stature omitting inflorescences) (mm); (6) seed mass (SM)(µg), and (7) root length (RL) (mm).

	Traits					
Species	SLA	LDMC	Root/shoot	Rep/veg	MPH	SM
Allium sphaerocephalon	13.32	232.20	0.10	0.19	675.00	1610.00
Alyssum simplex	16.62	306.13	0.12	0.14	25.94	398.52
Anagallis arvensis	24.29	203.55	0.26	0.26	60.09	455.04
Anchusa azurea	11.96	138.19	0.18	0.05	176.65	19200.00
Asteriscus aquaticus	24.56	170.36	0.09	0.30	162.07	229.50
Asterolinon linumstellatum	26.58	297.68	0.19	0.35	23.26	249.28
Astragalus stella	26.24	216.23	0.10	0.18	131.89	743.86
Bartsia trixago	13.13	243.54	0.09	0.44	225.94	37.58
Bombycilaena discolor	28.66	266.04	0.08	1.13	81.18	1342.45
Brachypodium phoenicoides	25.21	398.76	0.06	1.06	106.01	3200.00
Bromus rubens	28.52	270.60	0.11	0.43	129.38	519.40
Campanula erinus	24.21	212.55	0.09	0.50	69.08	19.52
Campanula fastigiata	34.56	144.38	0.05	1.32	23.93	8.42
Centaurea hyssopifolia	12.74	233.25	0.09	0.45	354.76	1031.70
Centaurea melitensis	18.63	293.24	0.07	0.41	282.90	1382.20
Centaurium quadrifolium	11.40	233.56	0.08	0.28	172.80	16.68
Centranthus calcitrapae	15.74	161.13	0.08	0.31	212.90	554.38
Cerastium glomeratum	24.10	149.32	0.13	0.05	7.51	46.26
Chaenorhinum reyesii	16.74	160.32	0.10	0.38	23.22	12.12
Cirsium sp.	17.16	246.37	0.09	0.46	252.52	891.98
Dipcadi serotinum	8.82	155.62	0.14	1.73	832.23	4210.00

Diplotaxis sp.	17.73	241.57	0.21	0.04	96.76	11313.73
Echium vulgare	11.06	222.15	0.10	0.25	279.15	2442.56
Erodium botryx	14.47	247.76	0.12	0.13	52.24	930.12
Erodium cicutarium	12.84	243.92	0.14	0.17	46.34	1940.82
Erodium pulverulentum	15.34	254.30	0.10	0.10	53.75	512.00
Eruca vesicaria	19.09	155.79	0.19	0.24	192.27	812.38
Euphorbia falcata	26.11	255.39	0.10	0.11	36.45	92.38
Euphorbia sulcata	27.47	279.75	0.21	0.03	13.44	213.52
Filago pyramidata	30.35	265.79	0.06	0.77	57.06	50.48
Frankenia sp.	17.45	243.51	0.17	0.28	65.89	282.43
Galium parisiense	17.65	331.08	0.07	0.47	177.68	170.30
Hedypnois cretica	27.99	165.68	0.07	1.15	88.15	1531.48
Helianthemum salicifolium	18.31	245.02	0.16	0.20	73.82	148.64
Helianthemum squamatum	6.26	255.36	0.29	0.01	323.98	53841.84
Herniaria cinerea	12.98	290.81	0.13	0.25	5.87	87.65
Hippocrepis ciliata	14.26	273.92	0.09	0.08	30.26	1113.93
Holosteum umbellatum	34.15	113.05	0.07	0.68	27.43	107.18
Hornungia petraea	26.82	179.27	0.16	0.58	25.35	58.24
Launaea fragilis	13.61	157.37	0.10	1.02	228.91	613.81
Leontodon taraxacoides	20.58	173.83	0.07	1.39	131.06	368.02
Lepidium subulatum	8.29	411.40	0.88	0.00	337.87	1.63596E+11
Limonium echioides	12.73	299.08	0.56	0.56	102.33	353.70
Linaria glauca	23.66	159.06	0.01	0.30	115.87	3.98
Lomelosia stellata	11.65	248.97	0.09	0.58	97.38	13698.06
Macrochloa tenacissima	3.03	595.83	0.09	0.14	1032.75	4970.00
Malva aegyptia	13.94	270.42	0.06	0.85	146.41	1097.32
Meconopsis sp.	21.51	238.19	0.06	0.50	72.67	124.47
Medicago minima	28.35	254.52	0.08	0.05	99.82	944.00
Mibora minima	52.34	152.05	0.13	0.75	20.47	100.00
Micropyrum tenellum	23.83	313.16	0.18	0.44	34.79	246.33
Minuartia hybrida	21.79	217.40	0.15	0.23	36.93	28.50

Neatostema apulum	14.44	262.07	0.11	0.05	94.96	992.24
Odontites longiflora	13.82	250.40	0.09	0.36	189.51	57.79
Papaver sp.	21.50	245.42	0.06	0.59	69.87	85.93
Pistorinia hispanica	12.60	56.35	0.06	0.36	77.75	16.38
Plantago afra	14.94	216.47	0.16	0.18	39.89	655.88
Platycapnos spicata	28.13	148.68	0.08	0.24	73.34	1138.15
Poa bulbosa	27.56	319.62	0.15	0.35	78.56	900.00
Reseda phyteuma	19.28	193.74	0.11	0.60	111.34	1190.00
Reseda stricta	9.24	300.20	0.14	0.32	311.40	342.33
Reseda suffruticosa	14.48	247.46	0.13	0.37	175.32	762.57
Sedum gypsicola	7.06	88.94	0.12	0.28	91.13	55.65
Senecio gallicus	18.37	144.83	0.30	0.30	138.15	250.00
Sherardia arvensis	27.16	222.88	0.12	0.13	46.15	2410.00
Sisymbrium runcinatum	17.59	250.73	0.21	0.03	89.91	14991.53
Stoibrax dichotomum	17.02	218.40	0.08	0.70	110.88	216.40
Teucrium capitatum	12.34	380.94	0.08	0.13	308.80	800.00
Trigonella polyceratia	18.88	280.85	0.10	0.06	143.69	760.00
Valerianella coronata	19.24	177.39	0.12	0.09	33.68	547.22
Vulpia ciliata	25.10	388.40	0.18	0.71	100.70	261.36
Ziziphora hispanica	17.11	272.38	0.15	0.21	87.05	210.82

CHAPTER 2

Disentangling the role of a perennial tussock forming grass in the assembly of semiarid gypsum plant communities: a field experiment controlling aboveground and belowground biotic effects

Laura Ortiz, Pablo Ferrandis & Arantzazu L. Luzuriaga

ABSTRACT

The facilitative effect of *Macrochloa tenacissima* plants on annual-dominated plant communities in semiarid climates has been extensively studied. Many studies suggest that the influence of this perennial tussock grass on surrounding microclimate conditions significantly determines the plant community assembling in their vicinity. However, there are still unanswered questions about the specific role played by the aboveground and belowground parts of the plant in combination with availability of propagules in the soil and with water availability. This study is the first attempt to study separately the effects of aboveground and belowground parts of *Macrochloa tenacissima* on the structure of annual-dominated plant communities in the semiarid gypsum system in Central Iberian Peninsula. To do so, we created in the field a factorial design combining four *M. tenacissima* scenarios, i.e. intact plants, alive laid down plants (belowground effect, hereinafter), dead standing plants (aboveground effect) and open areas, with two irrigation treatments (natural precipitation *vs.* irrigation treatment) and two seed availability treatments (seed free soil *vs.* homogenised natural soil with the complete seed bank). We sampled the annual-dominated plant community three years after the field experiment setup. In contrast to the spread idea that *M. tenacissima* can enhance plant survival and species diversity in Mediterranean drylands, our results showed a generally negative effect of *M. tenacissima* tussocks on annual plant communities. The belowground effect treatments showed that *M. tenacissima* exerted a negative effect on annual plant communities, probably related to belowground competition for resources. Moreover, the aboveground effect treatment only increased species richness in seed free soils with irrigation treatment. We can also conclude that there was no clear trait selection by the presence of *M. tenacissima* (or any of its parts). Our results confirmed the importance of seed availability in our systems, furthermore, we demonstrated that seed free soils required a longer time than expected to equalize in seed availability with natural soil seed banks which played an important role in the species richness, plant cover and trait selection in our annual-dominated gypsum system.

Keywords

Assemblage process, competition, facilitation, functional traits, gypsum systems, *Macrochloa tenacissima,* seed availability, water availability.

INTRODUCTION

Facilitation is a coexistence mechanism that has been extensively studied by plant ecology for years. The Stress Gradient Hypothesis (Bertness & Callaway, 1994) suggested the prevalence of facilitation in stress conditions over competition. Arid and semiarid systems are harsh environments where facilitation has been recognized as a major driving force of species coexistence in plant communities (Brooker et al., 2008; Michalet et al., 2006; Bertness & Callaway, 1994) and it is well known the key role of nurse plants in these ecosystems (Madrigal-González et al., 2020; Filazzola & Lortie, 2014; Luzuriaga et al., 2012). The concept of nurse plant refers to the capacity of certain species to enhance ecosystem function and species diversity by amelioration of the abiotic conditions (Madrigal-González et al., 2020; Gómez-Aparicio et al., 2004), benefiting other plants through a suite of direct and indirect mechanisms (Filazzola & Lortie, 2014; Brooker et al., 2008; Callaway, 2007). However, not all studies conducted in arid and semiarid systems point to facilitation. Some studies have obtained contrasting results (Armas & Pugnaire, 2011; Holmgren & Scheffer, 2010; Lortie & Callaway, 2006; Maestre et al., 2005). For example, Lortie & Callaway (2005) showed that facilitation increased with aridity, both spatially and temporally in a study reanalysing the data provided in Maestre et al. (2005) where they found that facilitation does not increase with stress in arid environments. Furthermore, facilitation is not the only mechanism involved in the formation of plant communities in harsh environments: competition also plays a key role (Hart & Marshall, 2013). Therefore, a better understanding of the prevalence of facilitation in stress conditions over competition is necessary to understand the process of species assemblage and species coexistence.

The vegetation formed mainly of *Macrochloa tenacissima* tussock are one of the most important and distinctive habitats of the semiarid systems in the Iberian Peninsula (Mota et al., 2017). *Macrochloa tenacissima* tussocks are usually distributed in patches, interspersed with open areas. The presence of these patches promotes spatial heterogeneity, which decisively influences the structure and composition of plant communities living in the area. For this reason, several studies have tried to explain the effects of *M. tenacissima* as a nurse plant (Luzuriaga et al., 2012; Maestre et al., 2007; 2001). *Macrochloa tenacissima* is a stress tolerant perennial tussock grass with a morpho structural and physiological characteristics to successfully colonise adverse semiarid Mediterranean environments (Maestre et al., 2007). Several studies point to the formation of "resource islands" around *M. tenacissima* tussocks by ameliorating microenvironmental conditions, which results in more fertile soil (Maestre et al., 2007), and higher water availability (Maestre & Cortina, 2005; Maestre et al., 2001). Maestre et al. (2001) demonstrated the positive interaction that *Macrochloa* plants exerted on the establishment of three Mediterranean shrub species (*Medicago arborea* L*., Quercus coccifera* L. and *Pistacia lentiscus* L.), as well as a net facilitative effect on *Lepidium subulatum* L. (Soliveres et al., 2010), a genuine gypsophilous shrub.

The architecture of *M. tenacissima* tussock plays a key role in the creation and maintenance of these islands of fertility*. Macrochloa* plants are able to act as a collector of runoff water after a rainfall event (Imeson & Prinsen, 2004; Puigdefábregas et al., 1999; Puigdefábregas & Sánchez, 1996), thus achieving greater infiltration near the plant base (Cerdà, 1997). Furthermore, aboveground parts of *Macrochloa* provide shade that can retain soil moisture at the soil surface, facilitating neighbours with shallower roots (Maestre et al., 2003) and also decreasing the vapour pressure difference between the beneficiary's leaves and the ambient air (Maestre & Escudero, 2009). However, if the amount of water consumed by *Macrochloa* tussocks is greater than the amount of water collected, then a direct competition for water with neighbouring plants can be activated (Maestre et al., 2003). Another important feature of *Macrochloa* is that a significant part of the biomass (61%) is formed by the root system, which can reach depths of more than 50 cm, being concentrated under the *Macrochloa* tussock at a depth of 10-20 cm (Maestre et al., 2007; Puigdefábregas et al., 1999). This shallow root system probably allows *Macrochloa* to respond quickly to sudden variation in soil water availability (Maestre et al., 2007; Ramírez et al., 2007). For all these reasons, we emphasize the importance of studying the independent effects of the aboveground and belowground components of this key perennial species on other plants in the vicinity, to better understand and predict its effects and the net role as a driver of assembly processes in drylands.

Seed availability in the soil seed bank is known to be crucial for annual plants in drylands and specially in gypsum system (Peralta et al., 2016; Olano et al., 2012; Caballero et al., 2008). Soil seed banks in our community are well structured, relatively homogeneous and abundant (Caballero et al., 2003; 2008). Seeds of annual species may remain in the seed bank in a dormant state instead of germinating to minimize the risk of a stress situation. This strategy is known as bet-hedging and consist of decreasing biological efficacy under normal or benign conditions in exchange for increasing efficacy under stressful conditions (Thompson, 2000, Venable, 2007). In addition, these seed banks are expected to recover quickly after destruction (Escudero et al., 2015; Martinez-Duro et al., 2012; Olano et al., 2012), due to the seed rain at small scales together with secondary dispersal from intact seed banks in the vicinity (Olano et al., 2012). Furthermore, *M. tenacissima* plants favor seed retention under their canopies during both primary and secondary seed dispersal events, which determines spatial seed bank heterogeneity (Bullock & Moy, 2004).

In semiarid systems water stress is the most critical environmental factor (Luzuriaga et al., 2012), showing a strong spatiotemporal variability (Holmgren et al., 2006; Whitford, 2002). In plant assembly processes, timing, and amount of water availability act as a primary filter eventually determining the species which will participate in the local realized assemblages (Vargas-Colin et al., 2022; Peralta et al., 2019; Peñuelas et al., 2004), so the presence of *Macrochloa* may act importantly as a secondary biotic factor modulating the effects of the primary abiotic filter (Luzuriaga et al., 2012). In this context, elucidating the extent of facilitative *vs.* competitive interactions of the below- and aboveground portions of *Macrochloa* is a major step to thoroughly understand the effect of dominant perennial plants on the assembly of plant community in drylands.

The study of functional diversity of experimental species assemblages represents an effective tool for understanding the processes involved in species assembly, being profusely used and refined in recent times (Sánchez et al., 2022; Peralta et al., 2019). Differences in trait values among coexisting species seems to favour fitness advantages, preventing competitive exclusion via niche partitioning (Ortiz et al., 2023). Therefore, knowing the functional trait patterns in the species sets that form our community assemblages may help us to understand the processes of facilitation or competition that are operating in our system in the face of abiotic and/or biotic factors.

In this study, we posed the following key questions about the role of dominant perennial plants in annual-dominated plant species assembly process of dryland gypsum systems combined with soil seed availability under two water availability treatments. Specifically, we wondered if *Macrochloa tenacissima* tussocks may benefit annual plant-dominated communities in terms of taxonomic and functional diversities. We aimed to unveil to which extent aboveground and belowground parts of *M. tenacissima* plants may differently affect the conformation of annual plant communities in their neighbourhoods and if irrigation and the subsequent relaxation of the abiotic filter may modulate the effects of grass tussocks on annual plant assembly. In this context, we evaluated to what extent did seed availability influence annual assembly processes in these semiarid systems. Specifically, we pose these hypotheses: 1) We expect that intact *M. tenacissima* tussocks will act as nurse plants and facilitate the establishment and development of the annual plant community, meaning that richness, cover and taxonomic diversity (i.e., complexity and productivity) would be higher close to intact tussocks than in open areas; 2) such facilitation effect mediated by the presence of intact *M. tenacissima* tussocks or parts of it (aboveground or belowground), as opposed to open areas, will enhance functional diversity, promoting thus the widening of the functional community ranges close to tussocks. Regarding the abiotic filter, we hypothesise that: 3) If *Macrochloa* mediated facilitation occurs specially in high abiotic stress situations (Bertness & Callaway, 1994; Callaway, 1994, 1997), we expect a higher facilitation effect in scenarios with natural precipitation than in scenarios where we have relaxed water stress through irrigation treatment. And, finally, 4) if *M. tenacissima* exerts a seed trapping effect consistent enough, we may expect that annual species assemblages grown on both seed availability scenarios (i.e., seed free soil vs. homogenized natural soil) would not have significant differences in terms of taxonomic and functional diversities after three years.

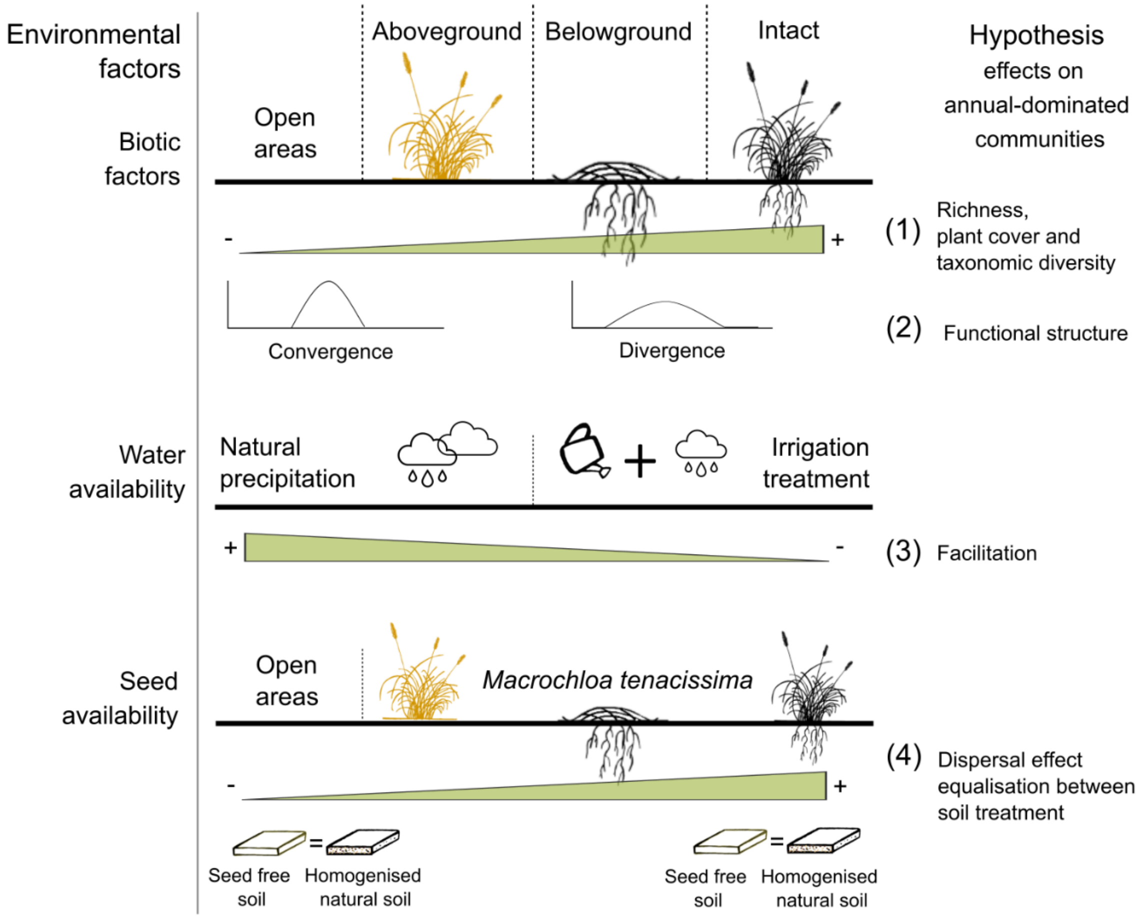


Figure 1. Conceptual scheme of the main hypotheses proposed: 1) We expect intact *M. tenacissima* tussocks act as nurse plants and facilitate the establishment and development of the community, which would mean that richness, cover and taxonomic diversity would be higher than in open areas; 2) This facilitation by the presence of intact *M. tenacissima* or parts of it (aboveground or belowground) will favour functional diversity, promoting the widening of functional ranges in the community. 3) We expect negative interactions to be more visible in plots with irrigation treatment, where we manipulated water stress to inhibit it, because it is expected that facilitation occur in high abiotic stress situations. 4) We expect a seed trapping effect of *M. tenacissima* which tends to equalize and enhance seed banks and assemblage features between the two seed availability scenarios (i.e., seed free soil vs. homogenized natural soil) under tussocks rather than in open areas.

METHODS

Study site

The field experiment was performed in Sotomayor Experimental Field Station (Aranjuez, central Spain, 40°01′55.7″N - 3°32′48.3″W, 590 m), located on a flat summit in a semiarid gypsum steppe. The climate is Mediterranean semiarid with 365 mm year^{-1} of average annual rainfall, 15°C of annual mean temperature and a marked summer drought which extends from May to August (Agencia Estatal de Meteorología, www.aemet.es). The plant community structure is defined by plant patches, where *Macrochloa tenacissima* strongly dominates the aboveground vegetation. *Macrochloa tenacissima* form dens, closed clumps, that usually grow up to 150 cm tall, occasionally reaching 200 cm. The plant forms long, narrow leaves, which are very flexible and strong, around 50 – 60 cm long (Pardo de Santallana, 2014). Accompanying *Macrochloa* tussocks we find some shrubby gypsophile specialists, such as *Helianthemum squamatum* (L.) Dum. Cours. *Lepidium subulatum* L. *Centaurea hyssopifolia* Vahl. and *Gypsophila struthium* L and a rich, dynamic annual plant community, where gypsophytes (e.g., *Chaenorrhinum reyesii* (C. Vicioso & Pau) Benedí and *Campanula fastigiata* Dufour ex Schult.) and gypsovags (e.g., *Alyssum simplex* Rudolphi, *Cerastium glomeratum* Thuill.) proliferate. Completing the mosaic, we found a well conserved biological soil crust mainly dominated by lichens as *Diploschistes diacapsis* (Ach.) Lumbsch, and *Squamarina lentigera* (G.H. Weber) Poelt, and gaps of bare soil.

Experimental design

This experiment was focused on testing the *Macrochloa tencissima* effects on the assembly of gypsum plant communities in two different scenarios of seed availability and two scenarios of water availability. To do that, we set up four field scenarios to test the effect of *Macrochloa tenacissima* (aboveground part, belowground part, complete plants, and open areas as control), two field scenarios of seed availability (seed free soil *vs*. homogenised natural soil) and two field scenarios of water availability (natural precipitation *vs.* irrigation treatment). The result is a complete factorial design with 16 experimental treatments 10-fold replicated, (i.e., 160 plots) (Figure 2).

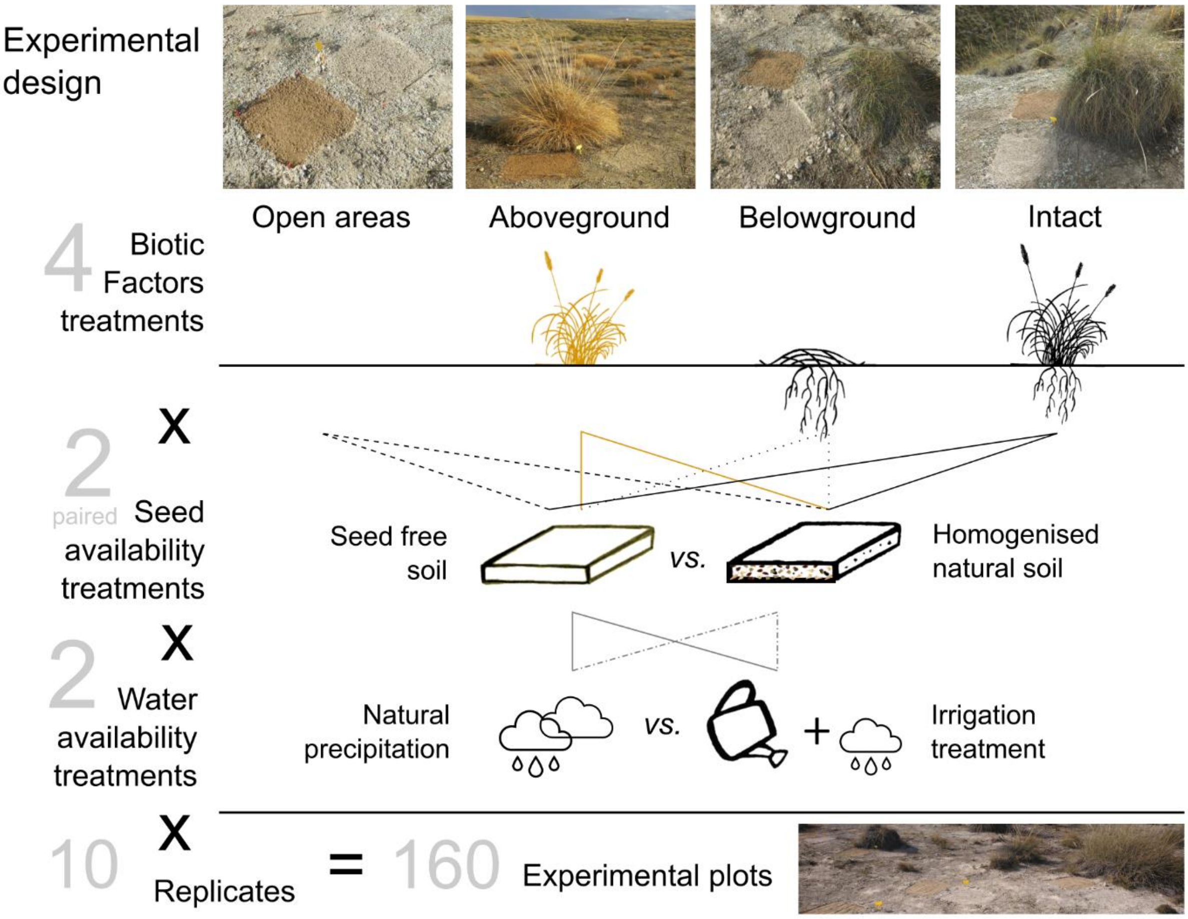


Figure 2. Scheme of the experimental design. Factorial design combining four field scenarios to test the effect of *Macrochloa tenacissima* (aboveground plant part, belowground plant part, complete plants, and open areas), two field scenarios of seed availability (seed free soil *vs*. homogenised natural soil) and two field scenarios of water availability (natural precipitation *vs.* irrigation treatment). The result is a complete factorial design with 16 experimental treatments 10-fold replicated, (i.e., 160 plots arranged in 80 plot pairs).

We used a paired design to test the effects of seed availability, built on the basis of two parallel 50 cm x 50 cm square plots in each experimental unit. Paired plots were separated by 10 cm, and each one filled, respectively, with seed free soil and with homogenised natural soil containing a good representation of the seed bank associated to the plant community in this system (seed free soil *vs*. homogenised natural soil). Firstly, we dug and removed the 3-cm deep topsoil from the plots in September 2018 because it is documented that, in semiarid areas, the upper 3-cm soil layer contains most of the viable seeds (Childs & Goodall, 1973). The soil extracted from the plots were mounded together and thoroughly stirred *in situ*, with a spade, to ensure soil homogenisation. With the soil stir operation we assure soil seed bank homogenisation even more, the species composition in these species-rich soil is spatially very similar (Peralta et al 2016; Caballero et al., 2008). In each experimental unit, one plot was filled with this homogenised natural soil. The other paired plot was filled with seed free soil collected from a gypsum quarry located near to the field station.

The *M. tenacissima* treatments were placed adjacent to mature individuals of *M. tenacissima,* at the south flank of the plant. Twenty paired plots were placed adjacent to *M. tenacissima* tussocks which were previously withered to dead, thus breaking any physiological activity of the plant. This treatment tries to evaluate the shading effects of *Macrochloa* tussocks regardless of its physiological activity. To do that, plants of *M. tenacissima* were fully, repeatedly sprayed with ecological vinegar ("Antical vinagre", produced by "FROSCH" in Barcelona) to stop vital metabolic processes. The spraying treatment was applied during three consecutive weeks once the vegetative cycle of the annual plant community was completed in July-August 2018 using a backpack sprayer. A pilot field test showed the efficiency of this treatment in interrupting any physiological activity of *Macrochloa* tussocks and the lack of residual effects on the plant community in next phenological cycle. We obtained prior formal permission to perform this operation. We called this treatment "aboveground effect". Twenty paired plots were placed adjacent to *M. tenacisssima* tussocks whose aerial part was anchored down to the opposite side using a metallic mesh, thus avoiding shading effect of *Macrochloa,* but maintaining its vital metabolic and physiological processes. We called this treatment "belowground effect". Other twenty paired plots were placed adjacent to mature intact individuals of *M. tenacissima.* We called this treatment "intact plants". We placed other twenty paired plots in open areas to act as control plots.

Finally, to test the influence of water availability as the main abiotic filter acting in semiarid Iberian gypsum systems (Luzuriaga et al., 2012), we performed two levels of water availability treatments. In each *Macrochloa* scenario, we randomly selected half of paired plots for the irrigation treatment, where 100% of the seasonal average rainfall from October to April was added manually (i.e., the life cycle period of annual plants in our system). The other half was assigned to the natural precipitation treatment (i.e., no additional watering). The irrigation treatment aimed to decrease the intensity of the abiotic filter and thus to explore the filtering effects of *Macrochloa* and its components (i.e., above- and underground ones) combined with different water availability levels. Mean precipitation recorded by Getafe meteorological station between 1981 and 2010 was 270 mm/m^2. Irrigation events were applied weekly (except when the rainfall in the corresponding week was higher than the historical average) fitting the seasonal distribution of average rainfall (see Appendix I for the calculations of the water quantities for irrigation). Moreover, we recorded the level of soil moisture in both water availability treatment using a Time Domain Reflectometer (Model TDR 100, Campbell Scientific) (see Appendix II).

Overall, our field experiment was performed in 160 plots i.e., (seed free soil *vs.* homogenised natural soil) x (natural rainfall *vs*. irrigation treatment) x (*M. tenacissima* intact vs. aboveground effect vs. belowground effect vs. open areas) x 10 replicates. (Figure 2). The experiment was run for a period of three consecutive years, in this study we will show the results of the last year, i.e., 2021, leaving so a reasonable time span for the consolidation of the expression of effects on assemblages from the experimental manipulation of factors (i.e., 2018). Although our study system typically shows highly variable yearly rainfall, 2021 can be classified as average, according to the 30-yr historical records in our reference weather station (see Appendix III).

Data and traits collection

In April 2021 we registered the number and visually the cover of species participating in the assemblage of each plot. We used a 50 cm x 50 cm frame divided into twenty-five 10 cm x 10 cm cells to facilitate counts, and we surveyed the central 30 x 30 cm to avoid edge effects. This sample size is sufficiently representative of our communities (Luzuriaga et al., 2012, 2015). For every plot, we calculated species richness, percentage of total plant cover, the inverse Simpson diversity index, and the evenness.

We included plant functional traits in our analyses. We used trait information from the database previously created by Peralta et al. (2019). This database resumes trait information about species in our plant community. The protocols to constitute this database followed those defined in Cornelissen et al. (2003). We selected functional traits related to fundamental ecological strategies (Westoby, 1998) linked to plant development and community assembly: (1) specific leaf area (SLA); (2) leaf dry matter content (LDMC); (3) root:shoot ratio (root/shoot; i.e., belowground:aboveground dry mass ratio); (4) reproductive ratio (rep./veg.; i.e., reproductive:vegetative dry mass ratio); (5) maximum plant height (MPH; i.e., plant stature omitting inflorescences), and (6) seed mass (SM). Trait information was available for 73 % of our species (see Appendix IV for species list). To estimate missing trait values (27%) we used *Rphylopars* (Goolsby et al., 2021) on the basis of the information obtained from the phylogenetic tree (Appendix V) built using *phylo.maker* function from the *V.PhyloMaker* package (Jin & Qian., 2019) and the *scenario 1* option to bind new tips (see Appendix VI for the values of each trait by species). Some traits (root/shoot, rep/veg, MPH and SM) were log transformed prior to statistical analyses.

For each assemblage, we calculated the community weighted mean (CWM) that has been confirmed to be particularly useful in the study of community structure and ecosystem properties (Lavorel et al., 2008; de Bello et al., 2005; Garnier et al., 2004, 2007), using the following formula:

$$CWM = \sum_{i=1}^{N} p_i \, x_i$$

where *N* is the number of species found in each assemblage, p_i is the proportional abundance (based on plant cover) of species *i* in the assemblage (ranging between 0 to 1), and x_i is the trait value of species *i*. We used the *dbFD* function from the *FD* package (Laliberté et al., 2014; Laliberté & Legendre, 2010).

We used the standardized mean pairwise dissimilarity index among species (SES.MPD) (Pavoine & Bonsall, 2011) as a functional diversity index. The SES.MPD is based on the Gower dissimilarities in trait values between all possible pairs of species coexisting in each pot, contrasting the observed MPD with 1000 null models calculated over all subsets of random species. It was calculated using the following formula:

$$SES.MPD = \frac{MPD_{observed} \quad - \ mean\ (MPD_{null)}}{mean\ (MPD_{null)}}$$

If values of SES.MPD are positive, means higher functional divergence, whereas if values are negative, indicate functional convergence in the realized species assemblage.

Statistical analyses

Generalized linear models (GLMs) were used to analyse species richness, plant cover, Inverse Simpson, and evenness of plant assemblages in our plots. We considered water availability treatment (natural precipitation *vs.* irrigation treatment), seed availability (seed free soil *vs.* homogenised natural soil) and biotic factors (*Macrochloa* aboveground and belowground parts, intact plants, and open areas), and the interaction between them as fixed factors.

We built PERMANOVA models to evaluate changes in the compositions of species, including biotic factors, water availability treatment and seed availability treatment as explanatory variables, as well as the interaction between them. Data were square root-transformed. We performed non-metric multidimensional scaling (NMDS) to visualize the differences in species composition among the four biotic and the two seed availability treatments.

We performed GLMs to explain variations in CWM and SES.MPD values for each functional trait (SLA, LDMC, root/shoot, rep/veg, MPH and SM). We considered water availability treatment (natural precipitation *vs.* irrigation treatment), seed availability treatment (seed free soil *vs*. homogenised natural soil) and biotic factors (aboveground, belowground, complete plants and open areas plots), and the interaction between them as fixed factors.

We used the *diversity* function from the *vegan* package (Oksanen et al., 2020) to perform inverse Simpson analysis. We used the *adonis* function from the *vegan* package (Oksanen et al., 2020) to perform PERMANOVA models. We performed Tukey HSD post-hoc test with *emmeans* function from the *emmeans* package (Russell, 2022). We used the *dbFD* function from the *FD* package (Laliberté et al., 2014; Laliberté & Legendre, 2010) to calculate CWM and the *ses.mpd* function from the *picante* package (Kembel et al., 2010) to calculate the standardized mean pairwise dissimilarity index among species (SES.MPD). All analyses were carried out with the R software version 4.0.5 (R Core Team, 2021).

RESULTS

Species richness, diversity, plant cover and species composition

We registered 53 species from 24 families in the assemblages of our experimental plots in spring 2021: 47 annuals, six perennials and six unidentified ones (see Appendix IV for the complete species list). Average plant cover per plot (30 x 30 cm) was 7.8%. Mean taxonomic diversity per plot (inverse Simpson index) was 2.57 and mean evenness 0.6. Both species richness and plant cover in assemblages were strongly affected by *Macrochloa* and initial seed availability treatments (Table 1 and Figure 3). In addition, plant cover was also influenced by interactions between *Macrochloa* and water and seed availabilities. Taxonomic diversity and evenness did not show any significant response to the manipulation of factors (Table 1).

In general, assemblages were richer (i.e., species number) and more productive (i.e., plant cover) in initially homogenized natural soil treatments than in seed free soil ones even three years after the experimental setup (Figure 3). This was particularly true for richness, which showed highest and lowest values, respectively, in open areas and intact *Macrochloa* tussock plots, while in experimentally manipulated tussock treatments it reached intermediate values (Figure 3). The highest cover values were recorded in open areas with homogenised natural soil, and in the aboveground effect treatments when irrigated. Remarkedly, in the initially seed free soil treatments, species cover, and richness still remained extremely low in every biotic and abiotic treatment three years after experimental implementation (Figure 3).

Biotic treatments and seed availability determined the species composition of assemblages three years after the starting of the experiment. Our model explained 19.4 % of the variance in species composition (Table 2). Seed free soil and homogenised natural soil showed the most outstanding differences in species composition. Species composition among biotic treatments showed that intact and belowground effects rendered similar species composition in the annual plant community, while aboveground effect was significantly different from the previous ones and more similar to open areas (Figure 4).

Table 1. Generalized linear models (GLMs) to analyse richness, total plant cover, Inverse Simpson, and evenness in experimental assemblages. Biotic factors (B; open areas, intact *M. tenacissima,* only belowground part and only aboveground part of *M. tenacissima*), water availability (W) and seed availability (S) treatments and their interactions were included in the model as fixed factors. Family distribution and link that best suited our models are indicated. Type III Wald Chi-square tests were indicated. Significant results are shown in bold, and significance indicated with asterisks: ***p<0.001; **p<0.01; *p<0.05; †p<0.1.

		Richness	Cover	Inverse Simpson	Evenness
	Error distr.	Poisson	Gaussian	Gaussian	Gaussian
	Link	log	identity	identity	identity
	Df	Chisq	Chisq	Chisq	Chisq
Biotic factors (B)	3	**11.3 ***	**27.8 *****	0.9	5.5
Water availability (W)	1	1.0	2.0	0.1	0.7
Seed availability (S)	1	**17.4 *****	**28.5 *****	1.1	3.2
B: W	3	0.5	**11.8 ****	1.4	2.9
B: S	3	0.9	**13.8 ***	0.4	0.5
W: S	1	0.9	0.5	0.0	2.5
B: W: S	3	1.8	6.6 †	0.1	2.9

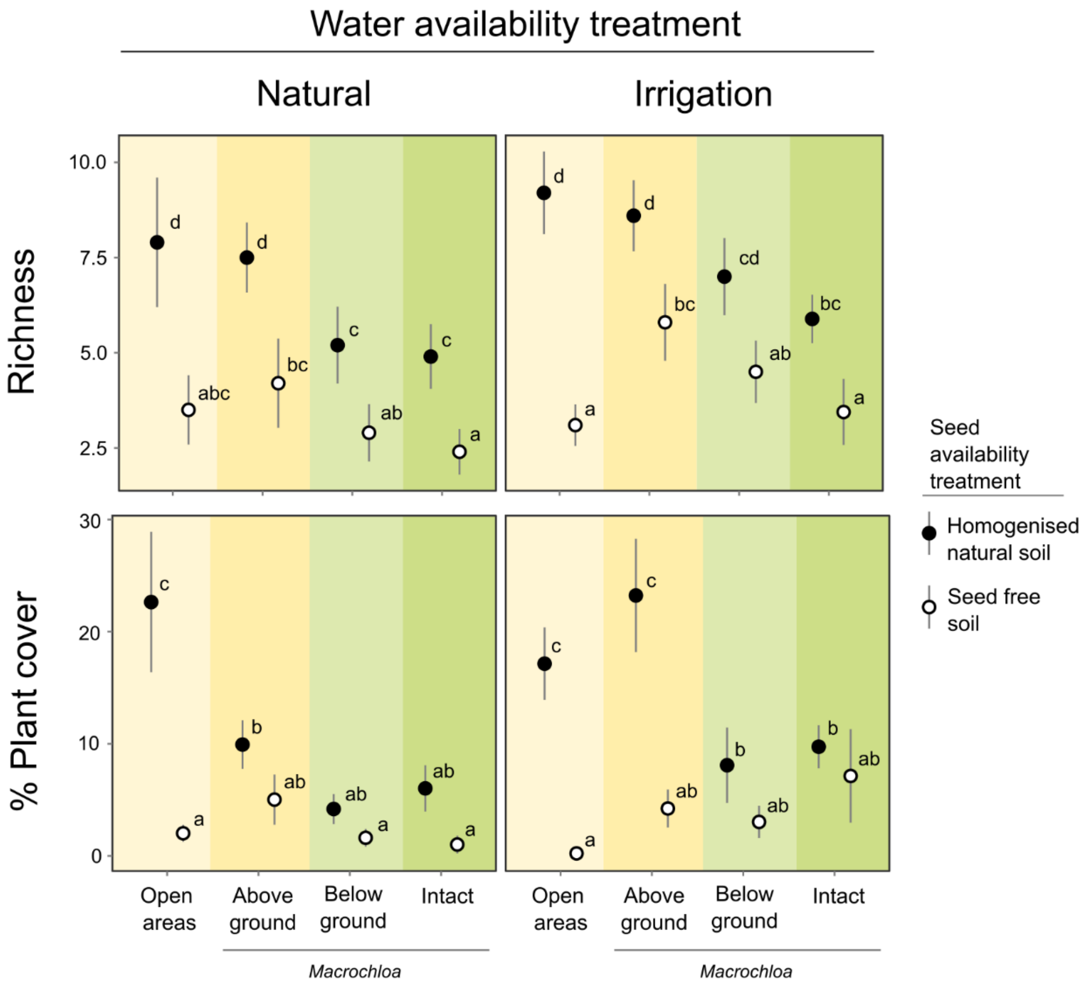


Figure 3. Representation of mean values (± standard error) of species richness and percentage of total plant cover in final assemblages. For each water availability treatment (natural precipitation *vs*. irrigation), different letters represent differences among *M. tenacissima* treatments and seed availability treatment (eight different scenarios) tested with estimated marginal means (package *emmeans*).

Table 2. PERMANOVA analyses to model the effect of water availability treatment (W), seed availability treatment (S), and biotic factors (B; bare soil, intact *M. tenacissima,* only belowground part and only aboveground part of *M. tenacissima*), and their interaction terms on species composition (n=237). The data were square root-transformed. Bray–Curtis dissimilarities were used. Type III sum of squares was used. Df: degrees of freedom.

	Df	F	R^2	p
Water availability (W)	1	1.5	0.01	0.1008
Seed availability (S)	1	12.1	0.07	**0.0001**
Biotic factors (B)	3	1.4	0.02	**0.0495**
W:S	1	1.0	0.01	0.4276
W:B	3	1.3	0.02	0.1215
S:B	3	1.1	0.02	0.2188
W:S:B	3	1.0	0.02	0.4162
Residuals	138		0.8	
Total	153		1.0	

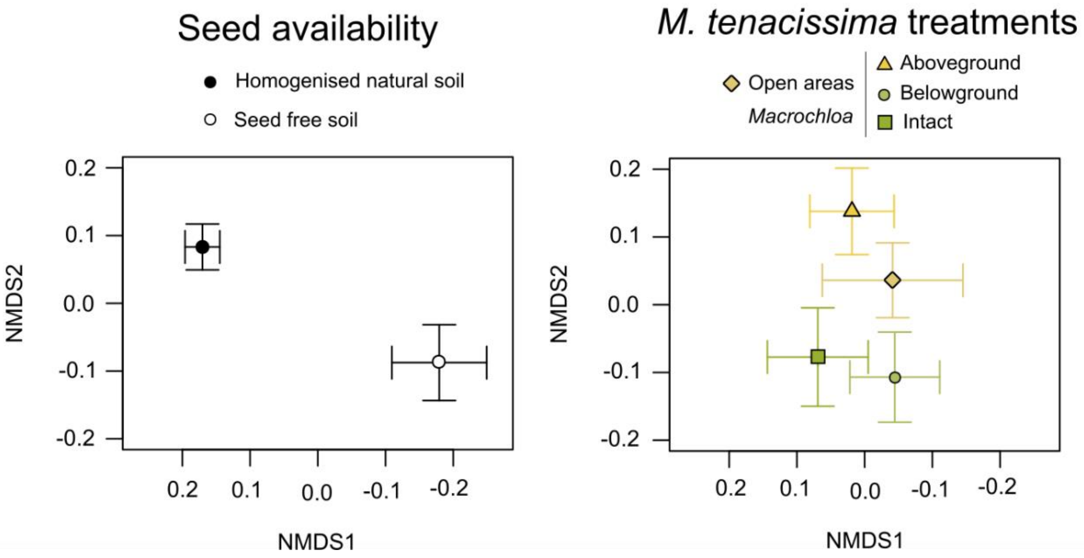


Figure 4. Non-metric multidimensional scaling (NMDS) ordination based on the species compositions in plots. Centroids and error bars for seed availability treatments the biotic factors (B; open areas, intact *M. tenacissima,* only belowground part and only aboveground part of *M. tenacissima*) and are shown. Differences between biotic factors are shown in the right panel, and differences between seed availability treatments are shown in the left panel.

Functional diversity

Seed availability was the major treatment determining functional patterns in our annual plant-dominated assemblages three years after the starting of the field experiment. Thus, this treatment significantly affected the root/shoot $_{CWM}$, SM $_{CWM}$, and veg/rep $_{CWM}$ (Table 3a) as follows: the former two were higher and the latter was lower in homogenized natural soil plots than in seed free soil plots (Figure 5a, b, c). Furthermore, the interaction between water availability and biotic treatments explained variation in SLA $_{CWM}$ (Table 3a), which overall was higher in irrigated than in natural rainfall plots, except in assemblages beneath intact *Macrochloa* tussocks, where the trend was the opposite (Figure 5d). The only MPD index that showed significant effects in response to the experimental factors was the MPH $_{ses.MPD.}$ This variable was significantly higher in intact *Macrochloa* comparing to the aboveground effect treatment (Table 3b and Figure 6).

Table 3. Generalized linear models (GLMs) to evaluate the effect of the experimental scenarios on a) community weighted mean (CWM), and b) mean pairwise distance index (MPD) values for plant traits. Biotic treatments (B; bare soil, intact *M. tenacissima,* only belowground part and only aboveground part of *M. tenacissima*), water availability treatment (W), seed availability treatment (S) and their interactions, were included in the models as fixed effects. Traits evaluated: specific leaf area (SLA); leaf dry matter content (LDMC); belowground:aboveground dry mass ratio (root/shoot); reproductive:vegetative dry mass ratio (rep/veg); maximum plant height (MPH) and seed mass (SM). Significant values are shown in bold, and significance indicated with asterisks: ***p<0.001; **p<0.01; *p<0.05; †p<0.1.

a) CWM		SLA	LDMC	Root/shoot	Rep/veg	MPH	Seed mass
	Df	Chisq	Chisq	Chisq	Chisq	Chisq	Chisq
Water availability (W)	1	2.1	0.4	1.1	1.7	2.7 †	2.7 †
Seed availability (S)	1	0.2	0.2	**6.9 ****	**4.0 ***	1.5	**5.5 ***
Biotic factors (B)	3	2.9	1.0	2.1	5.0	3.1	5.1
W:S	1	0.3	0.7	0.3	0.3	0.0	0.8
W:B	3	**10.6 ***	2.5	4.6	2.4	5.3	2.0
S:B	3	2.2	0.8	0.6	0.2	3.6	0.5

b) ses.MPD

		SLA	LDMC	Root/shoot	Rep/veg	MPH	Seed mass
	Df	Chisq	Chisq	Chisq	Chisq	Chisq	Chisq
Water availability (W)	1	2.1	0.5	0.6	0.4	1.5	0.0
Seed availability (S)	1	0.9	0.7	1.2	0.6	2.3	1.1
Biotic factors (B)	3	4.5	4.7	1.2	2.6	**7.9 ***	1.3
W:S	1	0.3	0.0	0.0	0.7	1.6	0.3
W:B	3	1.5	3.1	1.7	1.7	2.7	0.5
S:B	3	1.7	0.5	1.6	0.4	5.3	0.2

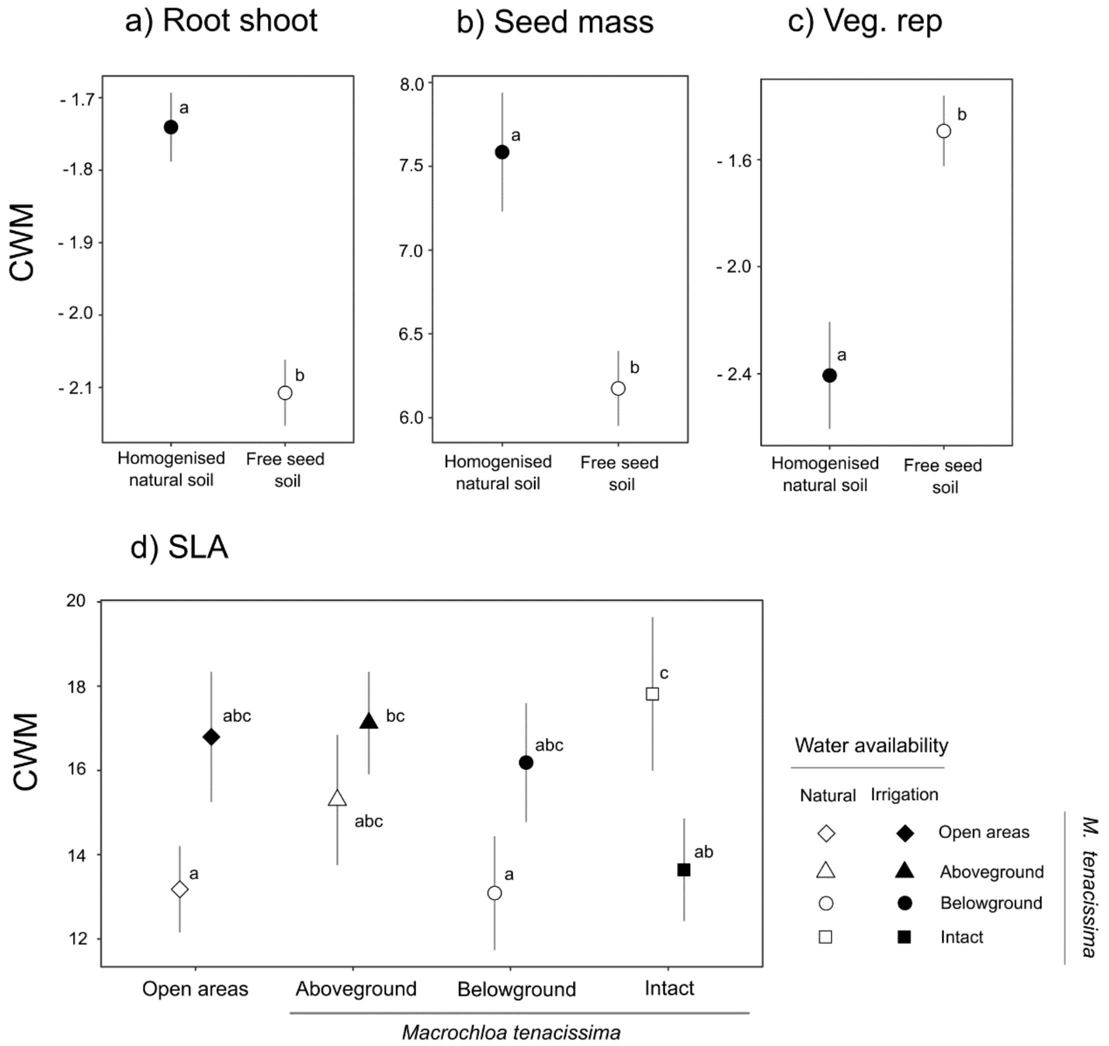


Figure 5. Mean values for community weighted means (CWM) for the significant terms shown in Table 3a: a) SLA, b) Root shoot, c) Veg.rep and d) Seed mass. Vertical bars represent standard errors. Different letters represent differences among treatments tested with estimated marginal means (package *emmeans*).

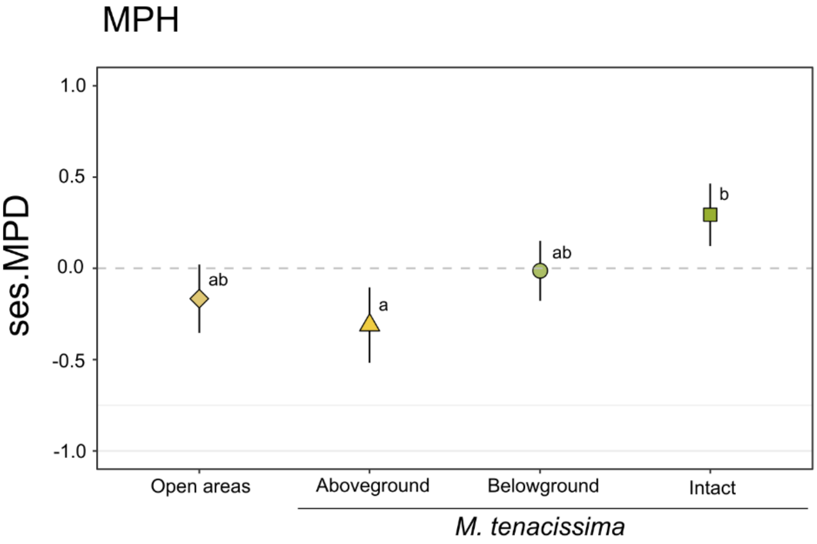


Figure 6. Mean values for standardized mean pairwise distance index (ses.MPD) for the significant term shown in Table 3b. Different letters represent significant differences among treatments tested with estimated marginal means (package *emmeans*).

DISCUSSION

The results obtained from this study allow us to a better understanding of the effects of *M. tenacissima* on annual-dominated plant communities, and how water and initial soil seed availability modulate this effect three years after the experimental setup. Our results suggest that intact *Macrochloa* plants did not play at all a net facilitating role in the formation of communities. On the contrary, *Macrochloa* alive tussocks seemed to compete for water with the annual species assemblages. In contrast, the physiologically inactive aboveground part of *Macrochloa* showed a positive shadow effect on the complexity and the productivity of assemblages, but only when water stress was reduced (irrigation treatment). Furthermore, we detected a functional trait selection, in terms of maximum plant height (MPH), in assemblages by the presence of *M. tenacissima*. Relaxation of the most important abiotic environmental filter in arid systems, water availability, did not result in noticeable effects in assemblages. After three years, the initial seed availability in the soil still defined decisively general assemblage features. Species richness between the two seed availability scenarios had not equalised in *Macrochloa* treatments yet, which in addition did not surpass that in open areas. Overall, those records may evidence the modest seed trapping effect of *Macrochloa* tussocks.

Although previous studies pointed to a nurse effect by *Macrochola tenacissima* in which shrubs living near *Macrochloa* plants had a higher survival rate than shrubs living in bare soil (Maestre et al., 2001), our results showed that *M. tenacissima* had a negative effect on richness and total plant cover of annual-dominated plant communities. Even though, fertile island created by presence of shrubs ameliorate abiotic conditions (Filazzola & Lortie, 2014; Wang et al., 2011; Yang et al., 2010), in our study, richness and percentage of plant cover was higher in open areas than in presence of *Macrochloa* plants. Previous studies already pointed to this possibility, suggesting that the relation between the supposed facilitator plant and the other species was not an advantage (Ramírez et al., 2007; Maestre et al., 2003). As for species richness, in our work we saw that when the *Macrochloa* plants are physiologically active, i.e., intact tussock and in belowground effect treatments, the species number in assemblages was lower than that in plots with no *Macrochloa* root activity, i.e., open area and aboveground plant fraction treatments. One possible explanation might be that if the competition mediated by the root system between annual plant-dominated assemblages and *Macrochloa* grass tussocks is operating, then the net result is not a facilitative effect in terms of richness and plant cover. As Maestre et al. (2003) suggested, if the amount of water consumed by *Macrochloa* tussocks is greater than the amount of water collected, exist the possibility of a direct competition for water between annuals and *Macrochloa.* Our results are in line with the conclusions of Luzuriaga et al. (2012), who pointed that although the established idea that shrubs usually act as nurses and are the main drivers of facilitative interactions in arid ecosystems, the effect of *Macrochloa* is generally negative in our annual-dominated community.

Although died, the aerial part of *Macrochloa* in the aboveground part treatment remains intact, so the rest of the species that grow around will benefit from the shade provided by the *M. tenacissima* clumps (Maestre & Escudero, 2009). As our results confirm, the shade is an important factor in plant-plant interactions in semi-arid environments (García-Camacho et al., 2017; Madrigal-González et al., 2020; Seifan et al., 2010). This will reduce evapotranspiration and keep more humidity in the soil, making it easier for the species to establish in its shelter. However, this is not the case in the scenarios where only the belowground part of *Macrochloa* remains intact but there is no aerial part, so we can assume that the competition generated between roots is greater than the facilitation that could be assumed (Maestre & Cortina, 2004; Kitzberger et al., 2000). In addition, there is evidence of situations where drought can be more severe in shade than without shade, a phenomenon known as dry shade (Valladares et al., 2004; 2001). There are no significant differences in plant richness and plant cover between scenarios with intact *Macrochloa* plants and with only the belowground part. Thus, we can assume that it is the aboveground part of the *Macrochloa* that is an advantage for the formation of gypsum annual plant-dominated communities. The high temperatures at which our species must live are a decisive factor and, although they are adapted to these high temperatures and the lack of water availability for long periods, the presence of a source of shade may benefit the richness of the community (and the cover if water is available, i.e., irrigation x *Macrochloa* aboveground part treatments). Furthermore, our results are consistent with the findings of Armas & Pugnaire (2011), where they found that belowground part of *Macrochloa* interferes with the development of the annual plant communities by depleting water availability in the zone of influence of *M. tenacissima*. Moreover, they pointed that this competition is diluted with increasing water availability. Luzuriaga et al. (2012) found that *Macrochloa* only exerted a net facilitative effect when water stress conditions were alleviated.

Contrary to our expectations, the seed bank did not recover in the three years that the experiment was active. Previous studies point to the rapid recovery of seed banks in semiarid systems (Escudero et al., 2015; Martinez-Duro et al., 2012; Olano et al., 2012), but in our case, our two soil scenarios showed differences in richness, percentage cover and species composition. The presence of a well-developed biological soil crust (BSC) brings heterogeneity to the soil and acts as a seed trap (Bowker et al., 2018; Zhang et al., 2016). Therefore, the absence of BSC in our seed free soil plots could be the reason why we have not observed such a recovery of the seed bank, in spite of the active horizontal secondary seed movements in this system (Martínez-Duro et al. 2012, 2009). Longer-term studies are needed to understand seed bank recovery in our system modulated by both abiotic and biotic components. Moreover, we found an effect on functional patterns of assemblages. In seed free soil scenarios, Root.shoot $_{CWM}$ and SM $_{CWM}$ values were lower than in homogenised natural soil scenarios, whereas the opposite was observed for Veg/rep $_{CWM}$ values. Those functional patterns in seed free soil assemblages may respond to the arrival of opportunistic species which could proliferate in a non-fully occupied space.

Although we expected that the presence of *M. tenacissima* and the improvement of microclimatic conditions around perennial tussocks would result in a functional divergence, our results did not show such an effect neither clearly defined trait selection patterns. Nonetheless, it was noteworthy the effect of irrigation on the SLA of the community. While in most cases the relaxation of this major abiotic filter slightly increased SLA of species participating in assemblages. Irrigation treatment substantially reduced SLA $_{CWM}$ under intact *Macrochloa* tussocks, evidencing one more time the intense root competition exerted by this perennial grass for water, which may be selecting for species with low SLA adapted to drought conditions in the near assemblages. Moreover, in open areas, species were shorter than species in presence of intact *M. tenacissima* plants. MPH values determine the competitive ability of species (Garnier et al., 2016), so probably species with high values of MPH increase the probability to survive in presence of *M. tenacissima* and compete for the resources.

In conclusion, we did not find that the presence of *Macrochloa tenacissima* exerted a facilitating effect in the annual plant-dominated communities in semiarid gypsum systems in the central Iberian Peninsula. On the contrary, the belowground part of *Macrochloa* seems to intensely compete for water and other soil resources with near plants, driving plant assembly in the vicinity. The aboveground part seems to exert some kind of shadow-mediated facilitation effect, but only when the stressful conditions of water availability are attenuated. The shade provided by *Macrohloa* may reduce evapotranspiration and maintain soil moisture, improving the richness and percentage of plant cover. Anyway, the balance effect of *M. tenacissima* perennial grass tussocks on assembly processes of annual plant-dominated communities in the vicinity may be overall dominated by the underground root competition over the aerial shading facilitative effects. Furthermore, we found no clear trait selection pattern by *M. tenacissima* tussocks (or any of its parts) on the assemblages. Contrary to our expectations, the seed bank takes longer to recover than expected, and *M. tenacissima* did not show seed trapping effects which significantly contribute to accelerate the process. Overall, our study points that *M. tenacissima* perennial grass tussocks, although may ameliorate microenvironmental conditions by aerial shading, do not provide a net nurse effect to annual plant-dominated communities actively proliferating in the Iberian gypsum systems.

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Supporting information

CHAPTER 2

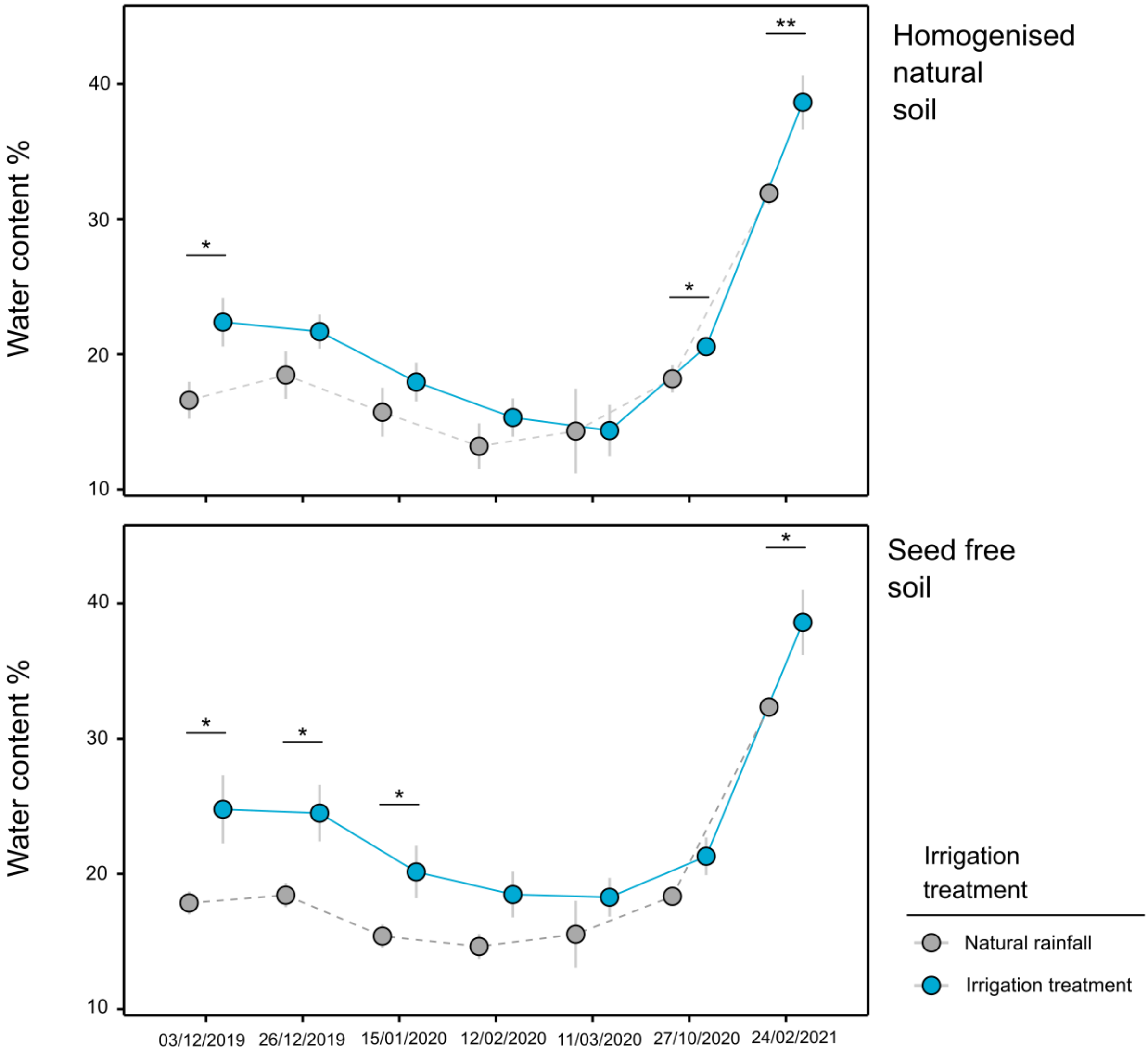
Disentangling the role of a perennial tussock forming grass in the assembly of semiarid gypsum plant communities: a field experiment controlling aboveground and belowground biotic effects

Laura Ortiz, Pablo Ferrandis & Arantzazu L. Luzuriaga

Appendix I. Table summarising the amount of water received each week in each plot. The information on precipitation is taken from the Getafe station, which provides the mean precipitation registered over 30 years (1981 - 2010).

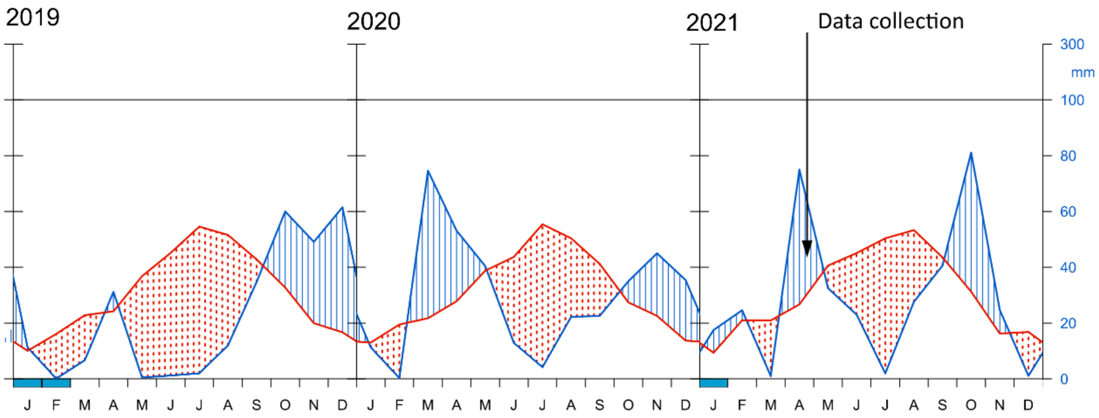
Month	Mean precipitation (mm)	Per week (l/m^2)	Per week ($l/0.25\ m^2$)	TOTAL
January	30.0	7.5	1.875	187.5
February	32.0	8	2	200
March	24.0	6	1.5	150
April	38.0	9.5	2.375	237.5
May	39.0	9.75	2.4375	243.75
June	19.0	-	-	-
July	9.0	-	-	-
August	9.0	-	-	-
September	22.0	5.5	1.375	137.5
October	50.0	12.5	3.125	312.5
November	48.0	12	3	300
December	45.0	11.25	2.8125	281.25

Appendix II. Mean values of the soil water content in plots in the irrigation treatment and natural rainfall (n= 112 in all cases) for the two soil availability treatments (homogenised natural soil and seed free soil) recorded during the experiment, measured by using a time domain reflectometry (TDR) method. Vertical bars represent standard errors.

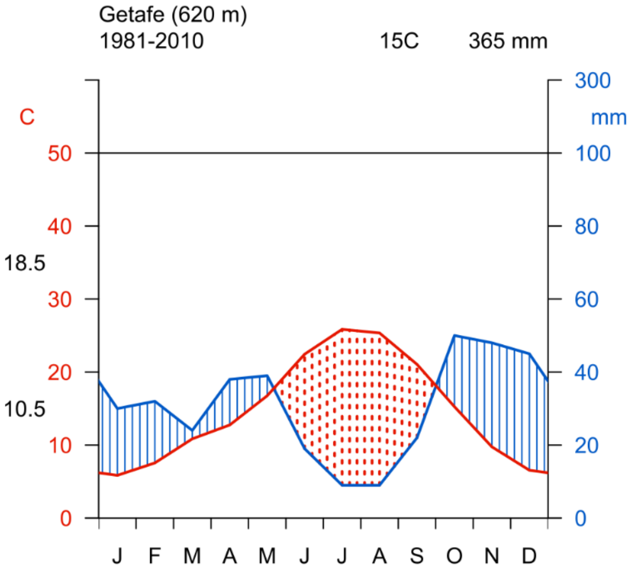


Appendix III. a) Climographs for the study site in Aranjuez (Madrid, Spain) for the three study years: 2019, 2020 and 2021. The black arrow indicates the data of data collection and b) average climograph for the 30-year 1981-2010 series in the nearest long term weather station from the study site (Getafe, Madrid).

a)



b)

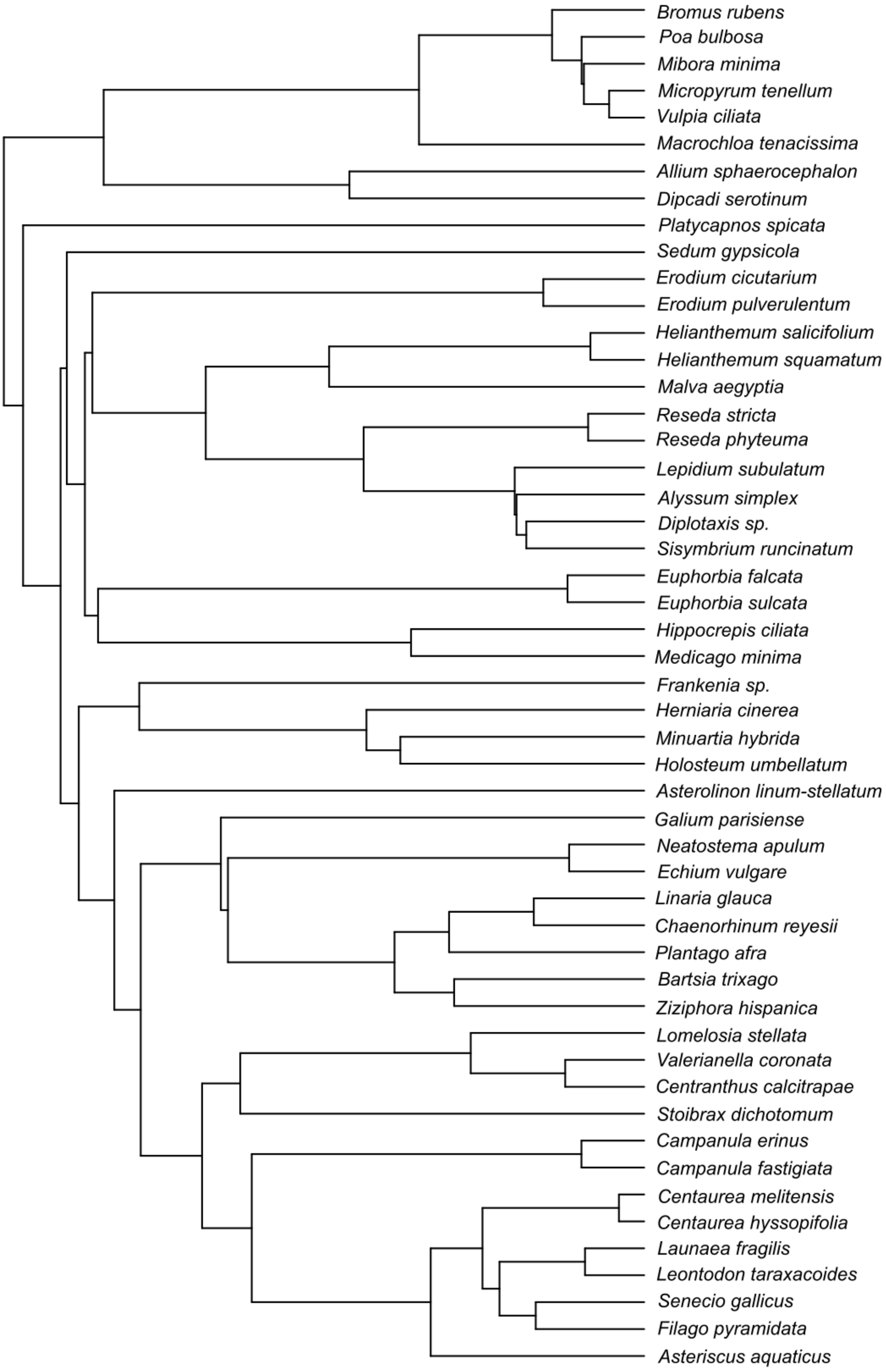


Appendix IV. Identified plant species recorded in the study area along the three study years (2019, 2020 and 2021). Botanic family and life cycle are indicated for each one.

Species	Family	Life cycle
Allium sphaerocephalon L.	Amaryllidaceae	Perennial
Alyssum simplex Rudolphi	Brassicaceae	Annual
Asteriscus aquaticus (L.) Less	Asteraceae	Annual
Asterolinon linum-stellatum (L.) Duby in DC	Primulaceae	Annual
Bartsia trixago L.	Orobanchaceae	Annual
Bromus rubens L.	Poaceae	Annual
Campanula erinus L.	Campanulaceae	Annual
Campanula fastigiata Dufour ex A.DC.	Campanulaceae	Annual
Centaurea hyssopifolia Vahl.	Asteraceae	Annual
Centaurea melitensis L.	Asteraceae	Annual
Centranthus calcitrapae (L.) Dufr.	Caprifoliaceae	Annual
Chaenorhinum reyesii (C. Vicioso & Pau) Benedí	Plantaginaceae	Annual
Dipcadi serotinum (L.) Medik	Asparagaceae	Annual
Diplotaxis sp.	Brassicaceae	Annual
Echium vulgare L.	Boraginaceae	Annual
Erodium cicutarium (L.) L'Her	Geraniaceae	Annual
Erodium pulverulentum (Cav.) Willd	Geraniaceae	Annual
Euphorbia falcata L.	Euphorbiaceae	Annual
Euphorbia sulcata Lens ex Loisel.	Euphorbiaceae	Annual
Filago pyramidata L.	Asteraceae	Annual
Frankenia sp.	Frankeniaceae	Annual
Galium parisiense L.	Rubiaceae	Annual
Helianthemum salicifolium (L.) Mill.	Cistaceae	Annual
Helianthemum squamatum (L.) Dum. Cours.	Cistaceae	Perennial
Herniaria cinerea DC. in Lam. & DC.	Caryophyllaceae	Annual
Hippocrepis ciliata Willd.	Fabaceae	Annual
Holosteum umbellatum L.	Caryophyllaceae	Annual
Launaea fragilis (Asso) Pau.	Asteraceae	Perennial
Leontodon taraxacoides (Vill.) Mérat.	Asteraceae	Annual
Lepidium subulatum L.	Brassicaceae	Perennial
Linaria glauca (L.) Chaz.	Plantaginaceae	Annual
Lomelosia stellata (L.) Raf.	Caprifoliaceae	Annual
Macrochloa tenacissima (L.) Kunth	Poaceae	Perennial
Malva aegyptia L.	Malvaceae	Annual
Medicago minima (L.) L.	Fabaceae	Annual
Mibora minima (L.) Desv.	Poaceae	Annual
Micropyrum tenellum (L.) Link.	Poaceae	Annual
Minuartia hybrida (Vill.) Schischk.	Caryophyllaceae	Annual
Neatostema apulum (L.) I.M.Johnst	Boraginaceae	Annual

Plantago afra L.	Plantaginaceae	Annual
Platycapnos spicata (L.) Bernh.	Papaveraceae	Annual
Poa bulbosa L.	Poaceae	Annual
Reseda phyteuma L.	Resedaceae	Annual
Reseda stricta Pers.	Resedaceae	Annual
Sedum gypsicola Boiss. & Reut.	Crassulaceae	Perennial
Senecio gallicus Vill.	Asteraceae	Annual
Sisymbrium runcinatum Lag. ex DC.	Brassicaceae	Annual
Stoibrax dichotomum (L.) Raf.	Apiaceae	Annual
Valerianella coronata (L.) DC.	Caprifoliaceae	Annual
Vulpia ciliata Dumort.	Poaceae	Annual
Ziziphora hispanica L.	Lamiaceae	Annual

Appendix V. Representation of species tree built using *phylo.maker* function from the *V.PhyloMaker* package (Jin & Qian., 2019) and the *scenario 1* option to bind new tips.



Appendix VI. Values of functional traits for plant species recorded in the study area. (1) specific leaf area (SLA)(mm^2/mg); (2) leaf dry matter content (LDMC)(mg/g); (3) root:shoot ratio (root/shoot; i.e., belowground:aboveground dry mass ratio); (4) reproductive ratio (rep./veg.; i.e., reproductive:vegetative dry mass ratio); (5) maximum plant height (MPH; i.e., plant stature omitting inflorescences) (mm) and (6) seed mass (SM)(μg).

Species	SLA	LDMC	Root/shoot	Rep/veg	MPH	SM
Allium sphaerocephalon	13.32	232.20	0.10	0.19	675.00	1610.00
Alyssum simplex	16.62	306.13	0.12	0.14	25.94	398.52
Asteriscus aquaticus	24.56	170.36	0.09	0.30	162.07	229.50
Asterolinon linumstellatum	26.58	297.68	0.19	0.35	23.26	249.28
Bartsia trixago	13.13	243.54	0.09	0.44	225.94	37.58
Bromus rubens	28.52	270.60	0.11	0.43	129.38	519.40
Campanula erinus	24.21	212.55	0.09	0.50	69.08	19.52
Campanula fastigiata	34.56	144.38	0.05	1.32	23.93	8.42
Centaurea hyssopifolia	12.74	233.25	0.09	0.45	354.76	1031.70
Centaurea melitensis	18.63	293.24	0.07	0.41	282.90	1382.20
Centranthus calcitrapae	15.74	161.13	0.08	0.31	212.90	554.38
Cerastium glomeratum	24.10	149.32	0.13	0.05	7.51	46.26
Chaenorhinum reyesii	16.74	160.32	0.10	0.38	23.22	12.12
Dipcadi serotinum	8.82	155.62	0.14	1.73	832.23	4210.00
Diplotaxis sp.	17.73	241.57	0.21	0.04	96.76	11313.73
Echium vulgare	11.06	222.15	0.10	0.25	279.15	2442.56
Erodium cicutarium	12.84	243.92	0.14	0.17	46.34	1940.82
Erodium pulverulentum	15.34	254.30	0.10	0.10	53.75	512.00
Euphorbia falcata	26.11	255.39	0.10	0.11	36.45	92.38
Euphorbia sulcata	27.47	279.75	0.21	0.03	13.44	213.52
Filago pyramidata	30.35	265.79	0.06	0.77	57.06	50.48
Frankenia sp.	17.45	243.51	0.17	0.28	65.89	282.43

Galium parisiense	17.65	331.08	0.07	0.47	177.68	170.30
Helianthemum salicifolium	18.31	245.02	0.16	0.20	73.82	148.64
Helianthemum squamatum	6.26	255.36	0.29	0.01	323.98	53841.84
Herniaria cinerea	12.98	290.81	0.13	0.25	5.87	87.65
Hippocrepis ciliata	14.26	273.92	0.09	0.08	30.26	1113.93
Holosteum umbellatum	34.15	113.05	0.07	0.68	27.43	107.18
Launaea fragilis	13.61	157.37	0.10	1.02	228.91	613.81
Leontodon taraxacoides	20.58	173.83	0.07	1.39	131.06	368.02
Lepidium subulatum	8.29	411.40	0.88	0.00	337.87	1.63596E+11
Limonium echioides	12.73	299.08	0.56	0.56	102.33	353.70
Linaria glauca	23.66	159.06	0.01	0.30	115.87	3.98
Lomelosia stellata	11.65	248.97	0.09	0.58	97.38	13698.06
Macrochloa tenacissima	3.03	595.83	0.09	0.14	1032.75	4970.00
Malva aegyptia	13.94	270.42	0.06	0.85	146.41	1097.32
Medicago minima	28.35	254.52	0.08	0.05	99.82	944.00
Mibora minima	52.34	152.05	0.13	0.75	20.47	100.00
Micropyrum tenellum	23.83	313.16	0.18	0.44	34.79	246.33
Minuartia hybrida	21.79	217.40	0.15	0.23	36.93	28.50
Neatostema apulum	14.44	262.07	0.11	0.05	94.96	992.24
Plantago afra	14.94	216.47	0.16	0.18	39.89	655.88
Platycapnos spicata	28.13	148.68	0.08	0.24	73.34	1138.15
Poa bulbosa	27.56	319.62	0.15	0.35	78.56	900.00
Reseda phyteuma	19.28	193.74	0.11	0.60	111.34	1190.00
Reseda stricta	9.24	300.20	0.14	0.32	311.40	342.33
Sedum gypsicola	7.06	88.94	0.12	0.28	91.13	55.65
Senecio gallicus	18.37	144.83	0.30	0.30	138.15	250.00
Sisymbrium runcinatum	17.59	250.73	0.21	0.03	89.91	14991.53
Stoibrax dichotomum	17.02	218.40	0.08	0.70	110.88	216.40
Valerianella coronata	19.24	177.39	0.12	0.09	33.68	547.22
Vulpia ciliata	25.10	388.40	0.18	0.71	100.70	261.36
Ziziphora hispanica	17.11	272.38	0.15	0.21	87.05	210.82

CHAPTER 3

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 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.

Keywords

Common garden experiment, functional diversity, gypsum soil system, maximum plant height, niche complementarity, plant assemblage, plant-lichen interaction, species coexistence

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.

MATERIALS AND METHODS

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 m2) 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).

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.

Experimental design

We conducted a factorial experiment at the CULTIVE facilities of Rey Juan Carlos University (Móstoles, Spain; https://urjc-cultive.webno de.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 (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 MPH values in assemblages). We calculated Rao indexes by the *dbFD* function in the *fd* 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 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 semi-arid 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).

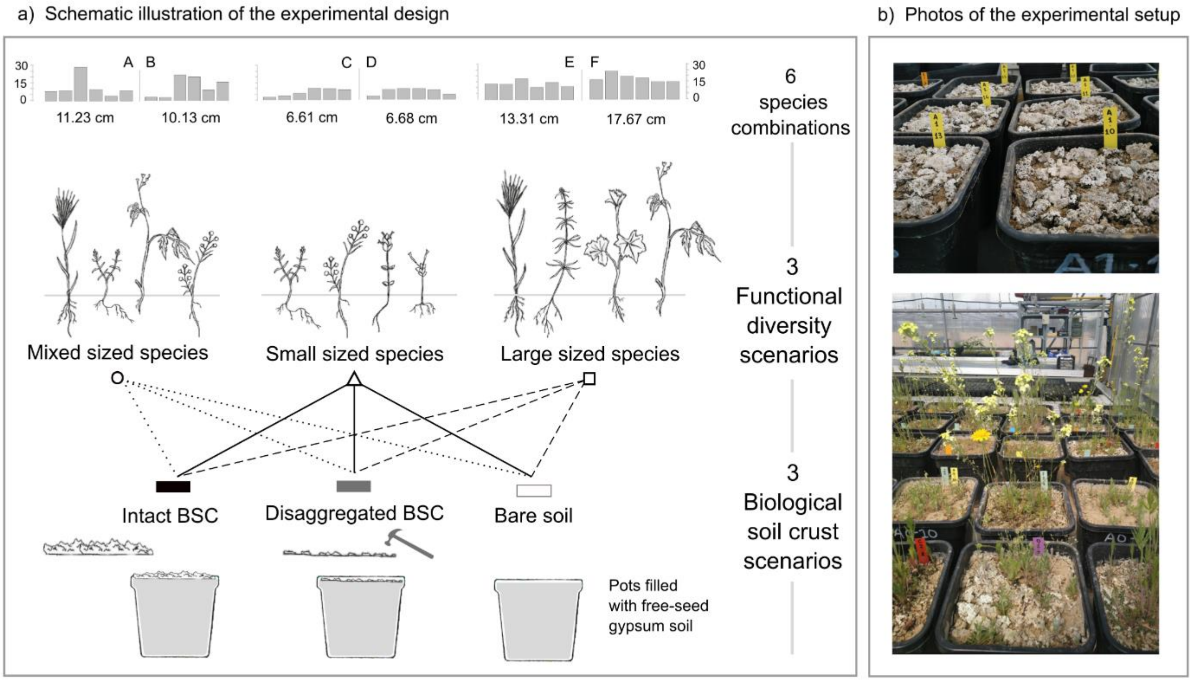


Figure 1. a) Schematic illustration of the experimental design. We designed three functional diversity scenarios, with initial assemblages formed by species with a wide range of maximum plant heights (MPH) (mixed sized species), or only by small or large sized species, each with two combinations of six 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 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 $_{\mathrm{MPH}}$ (see methods) for each functional scenario are also indicated.

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

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.

Statistical analyses

Plant abundance

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

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).

RESULTS

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).

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).

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

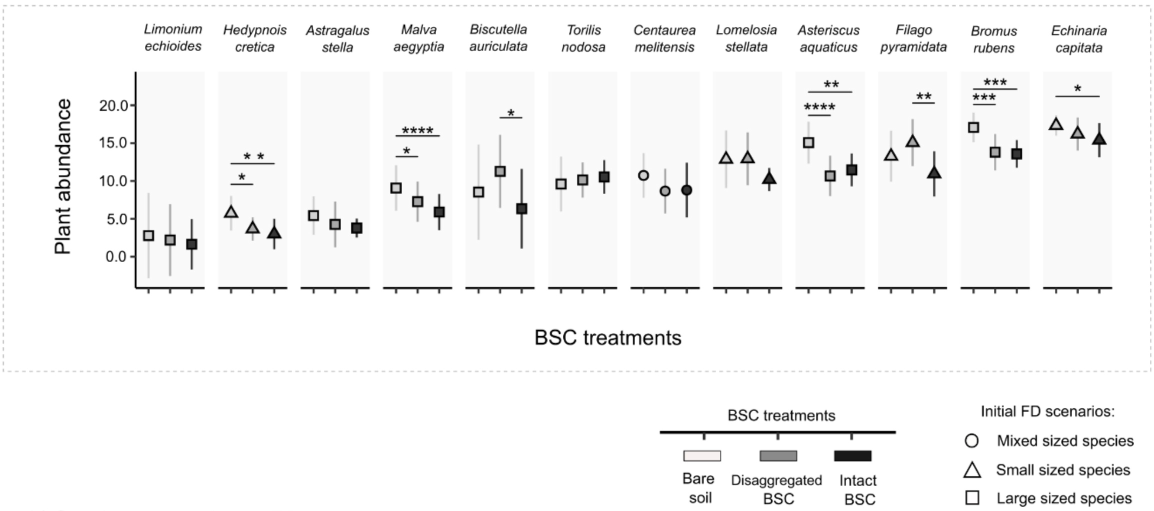
			Plant abundance	**Plant growth**	**Number of Fruits**
		Error distr.	Poisson	Gaussian	Gamma
		Link	log	identity	inverse
Species		Df	Wald Chisq	Wald Chisq	Wald Chisq
Asteriscus aquaticus	BSC	2	**12.942 ****	**24.271 *****	5.611
Astragalus stella	BSC	2	4.377	**19.389 *****	1.706
Biscutella auriculata	BSC	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

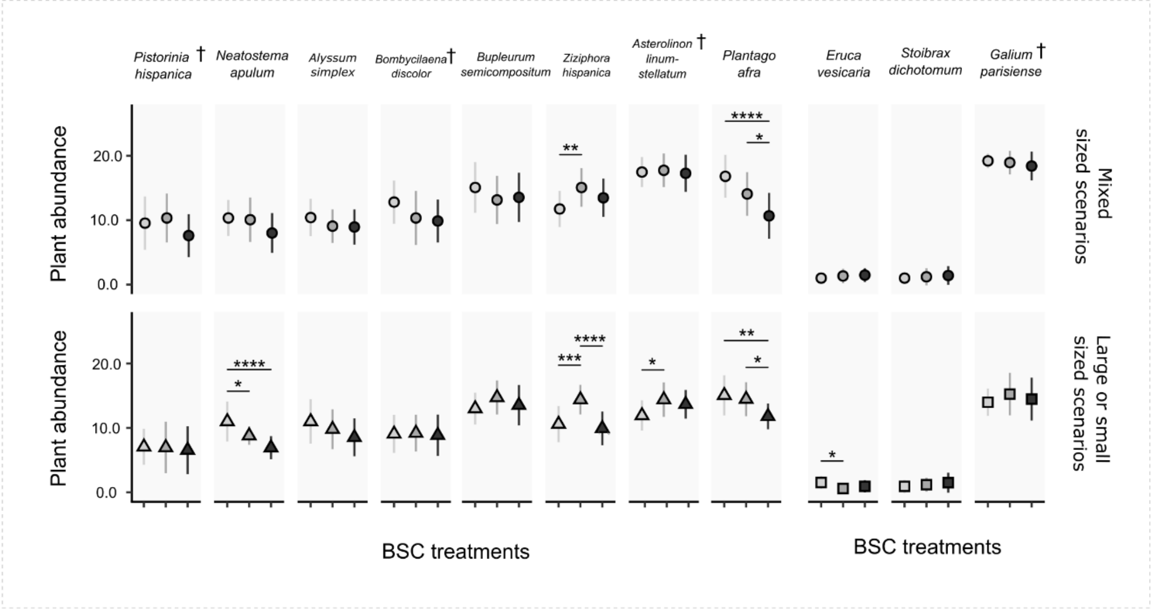
			Plant abundance	**Plant growth**	**Number of Fruits**
		Error distr.	Poisson	Gaussian	Gamma
		Link	log	identity	inverse
Species		Df	Wald Chisq	Wald Chisq	Wald Chisq
Alyssum simplex	BSC	2	4.686	4.584	**8.61 ***
	FD	1	0.252	0.397	0.011
	BSCxFD	2	0.591	0.473	1.119
Asterolinon Linum-stellatum	BSC	2	3.658	**85.713 *****	**197.186 *****
	FD	1	**15.715 *****	**8.094 ****	**73.944 *****
	BSCxFD	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
	BSCxFD	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
	BSCxFD	2	3.624	**14.241 *****	0.564
Eruca vesicaria	BSC	2	**6.514 ***	1.256	na.
	FD	1	1.697	**11.030*****	na.
	BSCxFD	2	**6.591 ***	5.546	na.
Galium parisiense	BSC	2	1.652	**30.699 *****	**15.08 *****
	FD	1	**16.447 *****	1.724	**11.077 ****
	BSCxFD	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 *****
	BSCxFD	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
	BSCxFD	2	2.349	**17.845 *****	1.256
Pistorinia hispanica	BSC	2	0.611	**15.066 *****	na.
	FD	1	**7.483 ****	0.502	na.
	BSCxFD	2	2.458	2.597	na.
Stoibrax dichotomum	BSC	2	1.902	**30.981 *****	3.857
	FD	1	0.038	0.000	**3.858 ***
	BSCxFD	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
	BSCxFD	2	3.444	4.732	1.624

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, 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: ****$p < 0.0001$; ***$p < 0.001$; **$p < 0.01$; *$p \leq 0.05$.

a) Species present only in one FD scenario

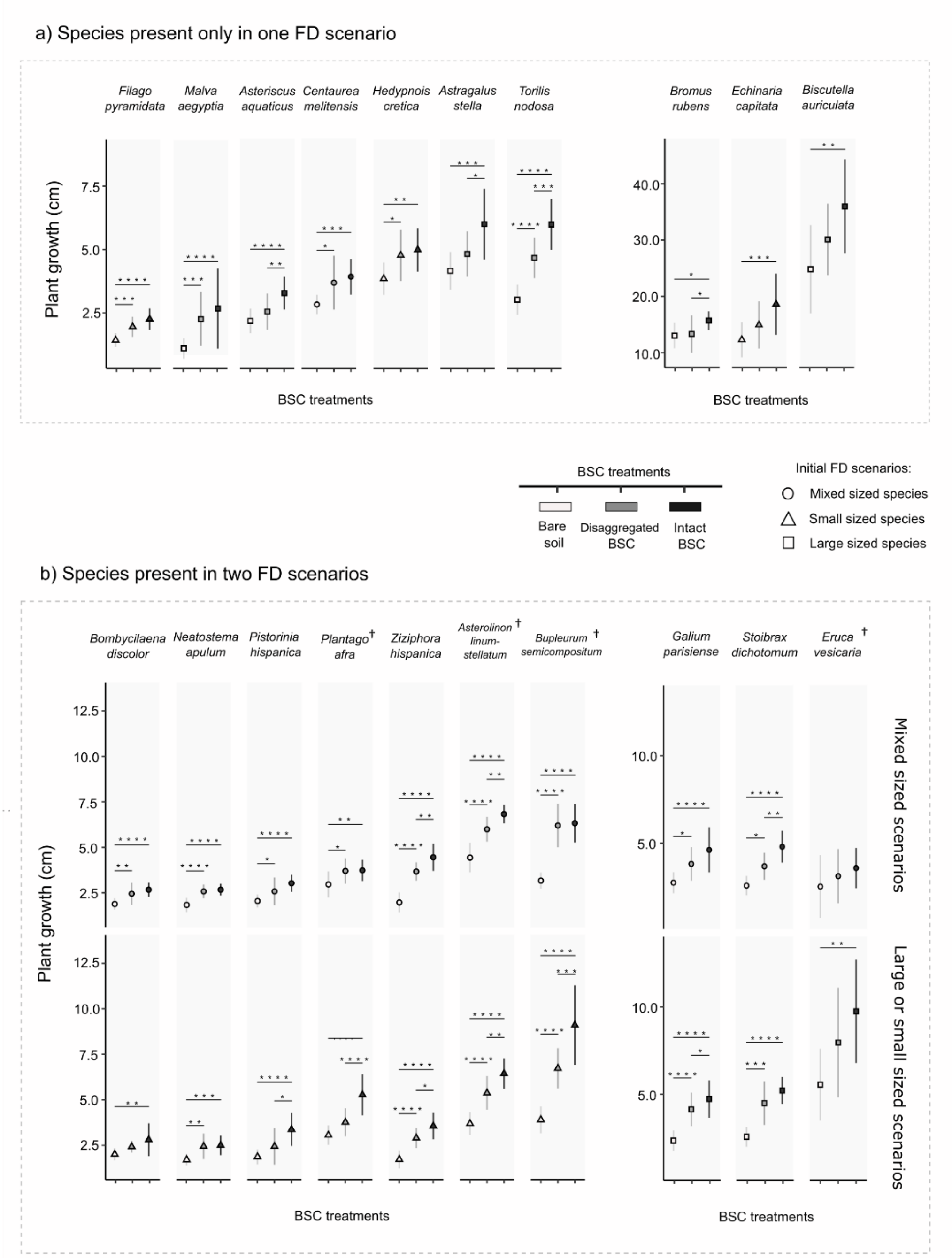


b) Species present in two FD scenarios



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

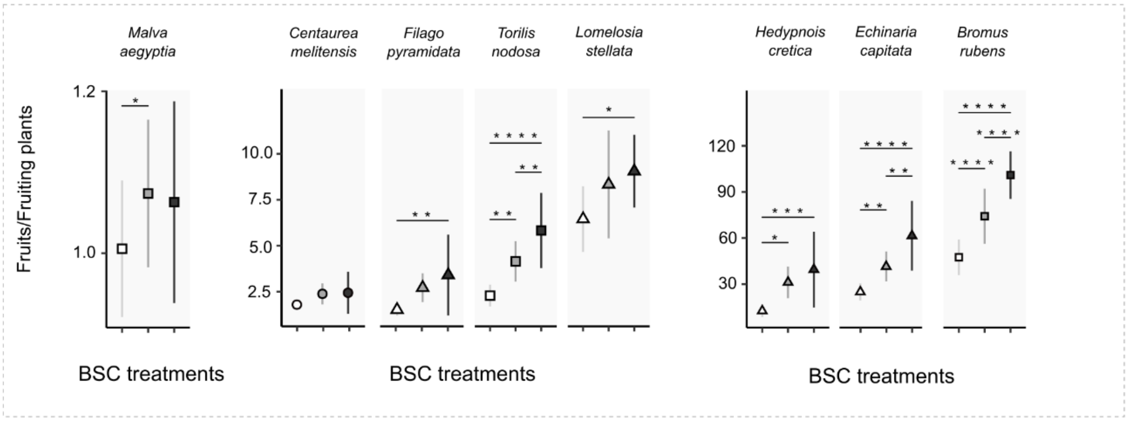
Figure 3. Mean plant growth measured as the vegetative stem height of the tallest individual per species in each pot at the vegetation development peak (March 2020). Species with significant differences between the biological soil crust (BSC) treatments or initial FD scenarios are presented (see Table 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: ****$p < 0.0001$; ***$p < 0.001$; **$p < 0.01$; *$p \leq 0.05$.



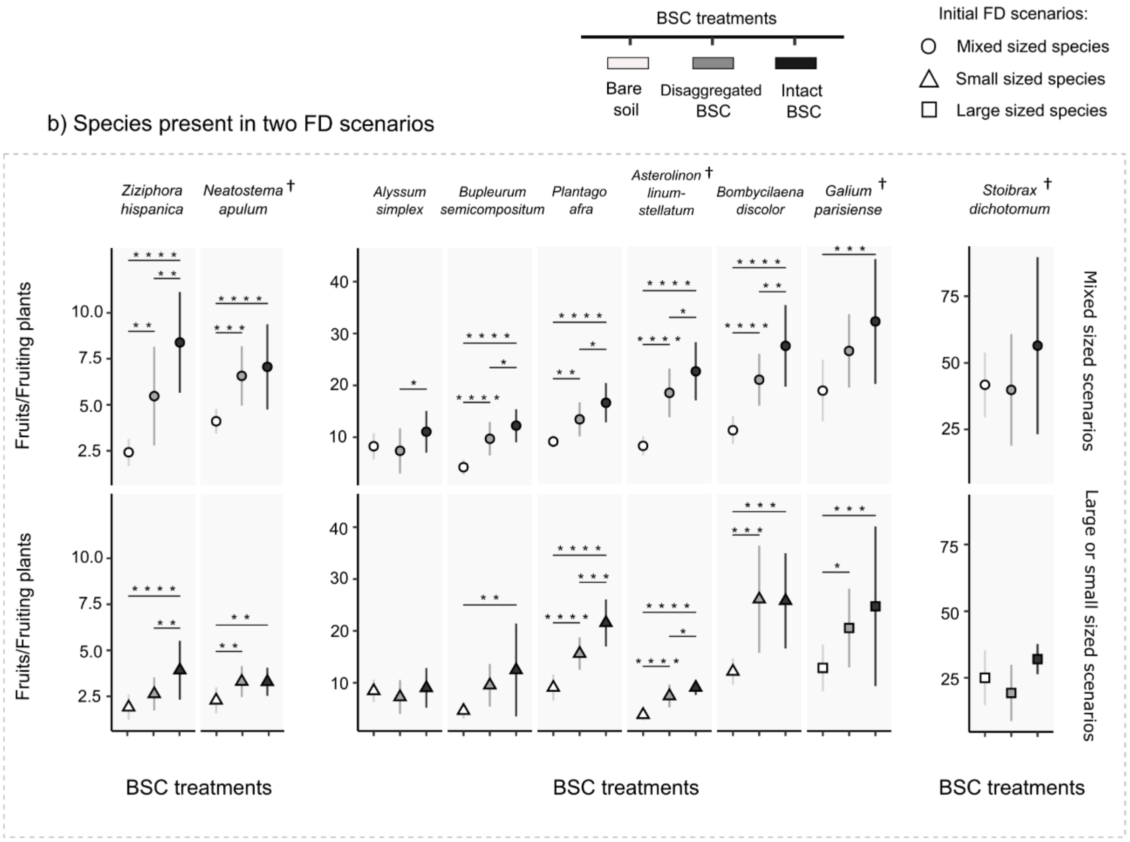
* Symbol † next to the species name indicates significant differences between low and high initiall functional diversity scenarios: see statistical analyses in Appendix III.

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: ****$p < 0.0001$; ***$p < 0.001$; **$p < 0.01$; *$p \leq 0.05$.

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.

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 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 evidencesupports the restrictive effects of BSC-forminglichens 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 inour 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 wáter 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.

The 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.

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Supporting information

CHAPTER 3

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

Laura Ortiz, Arantzazu L. Luzuriaga and Pablo Ferrandis

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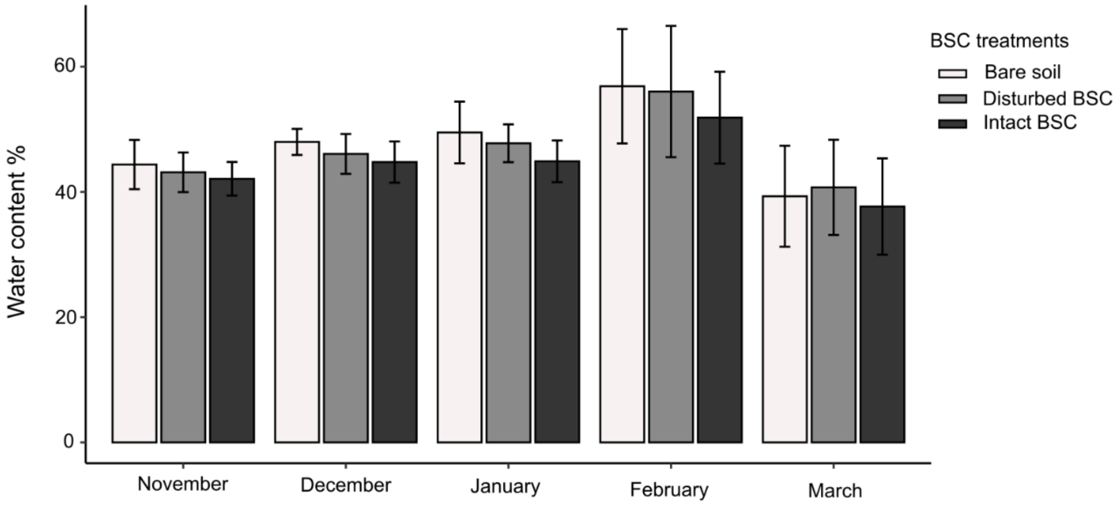
Appendix S1. (A) Pot soil water content in different biological soil crust (BSC) treatments, measured using a time domain reflectometry (TDR) method at 5 cm of depth soil. Vertical bars represent standard errors. (B) Table sowing results after performing a Tukey test to see differences between BSC treatments along time. Significant results are indicated in bold.

(A)



(B)

Date	BSC treatment	Estimate	p.adj
November	Bare-Disturbed	-1.24	0.633
November	Bare-BSC	-2.27	0.226
November	Disturbed-BSC	-1.04	0.724
December	Bare-Disturbed	-1.91	0.254
December	Bare-BSC	-3.22	**0.028**
December	Disturbed-BSC	-1.30	0.522
January	Bare-Disturbed	-1.73	0.523
January	Bare-BSC	-4.61	**0.016**
January	Disturbed-BSC	-2.88	0.175
February	Bare-Disturbed	-0.847	0.972
February	Bare-BSC	-5.02	0.376
February	Disturbed-BSC	-4.17	0.506
March	Bare-Disturbed	1.42	0.896
March	Bare-BSC	-1.64	0.865
March	Disturbed-BSC	-3.06	0.606

CHAPTER 4

Phylogenetic and functional diversities offer complementary information to disentangle species assembly processes in experimental gypsophilous annual plant assemblages.

Laura Ortiz, Pablo Ferrandis, Laura Rodríguez and Arantzazu L. Luzuriaga

ABSTRACT

Phylogenetic and functional diversities of coexisting species are powerful tools to understand the process of community assembly. Although many observational studies have demonstrated the effect of environmental variables on the functional and phylogenetic diversity of the resulting assemblages, there is a lack of knowledge about the causal relationships among phylogenetic and functional diversity in assembly mechanisms by directly manipulating the phylogenetic and functional diversity of whole assemblages. We designed a common garden trial in which we manipulated the initial phylogenetic diversities in experimental annual plant assemblages by combining species in groups of four to establish eleven combinations of annual plant species. Subsequently, we registered the resulting functional diversities for three key functional traits (i.e., seed mass; SM, specific leaf area; SLA, and maximum plant height; MPH) and a multi-trait response. Following a full crossed factorial design, each species combination scenario received two irrigation treatments: the mean monthly rainfall of the reference station (average) and one-third of the mean rainfall (drought). Our results demonstrated the importance of neighbourhood in the reproductive success and the ability to complete their life cycle of annual plant assemblages. Under average irrigation conditions, most plants fructified independently of their phylogenetic or functional neighbourhoods. However, plants growing in higher phylogenetic diversity scenarios fructified earlier and thus completed their life cycle earlier than in scenarios with low phylogenetic diversity. On the other hand, under drought conditions, more plants were able to fructify in high phylogenetic diversity scenarios and furthermore, they produced more seeds per fruit than in low phylogenetic diversity scenarios. Therefore, phylogenetically more diverse communities seem to be more resilient to water stressful events. Remarkably, our study demonstrates that phylogenetic diversity is an excellent predictor of the complementarity mechanisms that are occurring during species assembly processes. Furthermore, by including functional diversity in the form of a multi-trait index, we were able to explain some of the variability in the reproductive success of our community, confirming the complementarity of information provided by functional and phylogenetic diversity.

Keywords

Annual plants, community assemblage, gypsum systems, functional diversity, niche complementarity, phylogenetic diversity, reproductive success, water stress.

INTRODUCTION

Species assembly processes have received great attention in the last few years (Keddy & Laughlin, 2021; Garnier et al., 2016; Kraft & Ackerly, 2014; Götzenberger et al., 2012; HilleRisLambers et al., 2012). Functional and/or phylogenetic properties of the community are likely to inform about the environmental filtering and species-coexistence mechanisms operating during the assembly process (Cadotte et al., 2013). Indeed, most studies use the observed functional (Cera et al., 2022; Shipley, 2010) and phylogenetic (Sánchez et al., 2022; Luzuriaga et al., 2020; Muñoz et al., 2017; Kraft et al., 2007) patterns of the local assemblages to deduce the most likely ecological drivers occurred during the assembly process. Overall, environmental restrictions would cause convergence of functional strategies in the local assemblage, contrarily to plant-plant competition that is expected to result in divergent functional strategies of coexisting species according to the limiting similarity theory (Cadotte, 2017). In this line, phylogenetic relatedness among coexisting species has been used as a valuable tool to represent the deep ecological differences among coexisting species (Staab et al., 2021; Cadotte et al., 2008, 2009, 2012), which would integrate functional strategies beyond morphological functional traits (such as metabolic responses, phenological plasticity, etc.), very tough, if not unfeasible, to be measured (Cavender-Bares et al., 2009; Emerson & Gillespie, 2008; Kraft et al., 2007). This focus has greatly improved our understanding on plant community ecology. However, the use of phylogenetic diversities to understand coexistence among species has been controversial (de Bello et al., 2015; Godoy et al., 2014; Cavender-Bares et al., 2009). Some authors argue that evolutionary relatedness among species cannot predict niche differences (Godoy et al., 2014), while they detected phylogenetic signal on species' average fitness in an experimental setup based on pairwise species combinations to evaluate competition, which may favour coexistence between more closely related taxa (Mayfield & Levine, 2010). To the best of our knowledge, only Chaves et al. (2021) have experimentally manipulated whole plant species assemblages to obtain known initial phylogenetic diversities, in order to evaluate drivers of coexistence. Specifically, they demonstrated that the performance of annual plants living in neighbourhoods with high phylogenetic diversity was higher than that of individuals living in neighborhoods of phylogenetically related species. This response pattern was exacerbated under drought conditions, which overall evidenced niche complementarity as a major coexistence mechanism in annual plant communities of semiarid systems.

In this context, it is imperative to go beyond observational approaches (Götzenberger et al., 2012; HilleRisLambers et al. 2012) and to jointly manipulate initial phylogenetic and functional diversities to gauge the relative contribution of both community descriptors to species coexistence and eventually to assembly processes. In this study, we aim to disentangle the independent and interactive effects of phylogenetic and functional structure of multispecies experimental assemblages on plant performance and fitness and eventually on the main assembly processes. To this aim, we setup multispecies assemblages creating a gradient of eleven phylogenetic diversities, then each combination was characterized in terms of their functional diversities based on the three main axes of ecological strategies for plants (Garnier et al., 2016; Westoby, 1998): photosynthetic efficiency (specific leaf area, SLA), reproductive investment and dispersal ability (seed mass, SM) and competitive ability for light (maximum plant height, MPH). To the best of our knowledge, this is the first time that such a long range of phylogenetic diversity values (ranging from 0.23 to 0.93 PSV values) is implemented in experimental species assemblages and furthermore, this is the first study that evaluates the combined effect of experimentally manipulated phylogenetic and functional diversities on plant species fitness of coexisting species.

Annual plant communities in semiarid gypsum systems of the Tagus valley are excellent model systems to manipulate experimental assemblages (Sánchez et al., 2022; Chaves et al., 2021; Peralta et al., 2019; 2016), mainly because given their small size and short life cycles, we can use common garden techniques at small spatial scales and relatively short time lapses, compared to perennial plants. In this study system, water availability is known to be crucial for plant-plant interactions, and usually water limitation promotes competitive interactions among coexisting annual plant species (Luzuriaga et al., 2012). Thus, we expect that under water restriction conditions the effect of niche complementarity and/or the effect of competitive interactions among coexisting species would be exacerbated. The main objectives of this study are twofold: on the one hand, to assess the main ecological processes driving species assembly in our model community and on the other hand, to resolve the long-lasting issue about the relative contribution of phylogenetic *vs.* functional structure of plant communities to understand the ecological processes that drive species assembly. Specifically, for the first objective, we pose two alternative hypotheses: 1a) if phylogenetic or functional relatedness predicts differences in niche requirements of coexisting species, then we expect that in the most functionally and/or phylogenetically diverse assemblages, plants would be more likely to fructify and set more seeds; 1b) on the contrary, if phylogenetic or functional relatedness predicts the differences in competitive ability of coexisting species, then we expect that in the most functionally and/or phylogenetically diverse assemblages, competitive exclusion would be the dominant process resulting in lower plant fitness. Furthermore, we aim to disentangle the relative contributions of phylogenetic and functional structure of the experimental communities on the performance of the coexisting species. For this objective we propose three hypotheses: 2a) if phylogenetic distance between species is a comprehensive parameter that summarizes niche differences between species beyond concrete functional traits, we expect that phylogenetic diversity of the assemblages will explain better the differences in species performance than the diversity of each key functional trait separately or even that of the three functional traits combined, 2b) if functional diversities based on the three major components of ecological strategies for plants are representative of the ecological drivers determining species coexistence, then these parameters may explain most of the differences in species performance; and 2c) if functional and phylogenetic diversities are complementary components of community properties, then we expect that each parameter will explain meaningful fractions of the variability in species performance (see conceptual framework in Figure 1).

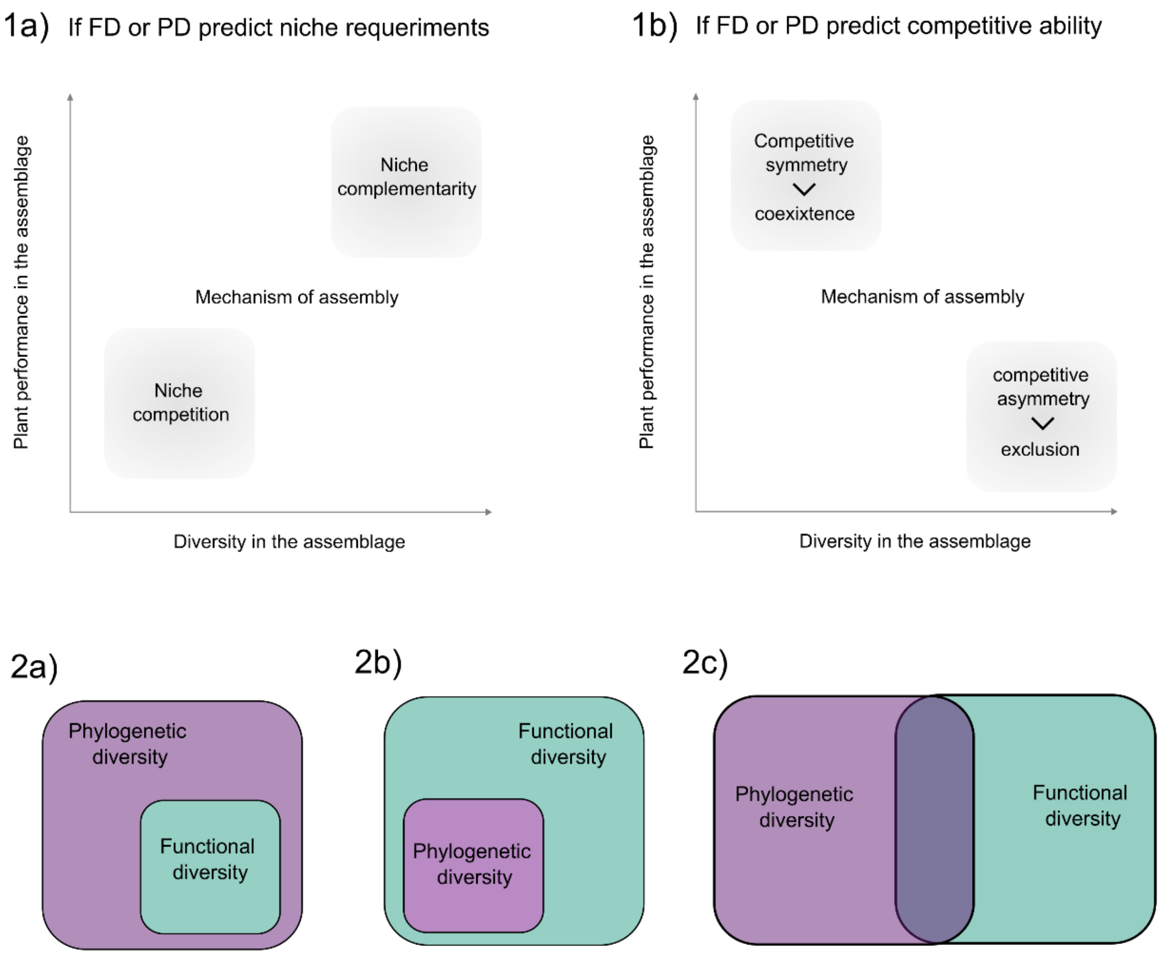


Figure 1. Conceptual framework for our hypotheses. 1a) if phylogenetic or functional relatedness predicts differences in niche requirements, we expect that in the most functionally (FD) and/or phylogenetically (PD) diverse assemblages, plants would be more likely to fructify and set more seeds; 1b) if phylogenetic or functional relatedness predicts the differences in competitive ability, we expect that in the most functionally and/or phylogenetically diverse assemblages, competitive exclusion would be the dominant process resulting in lower plant survival and fitness. 2a) if phylogenetic position summarizes the species niche beyond concrete functional traits, we expect that PD will explain better the differences in species performance than the diversity of each key functional trait separately or even that of the three functional traits combined; 2b) if FD are representative of the ecological drivers determining species coexistence, then these parameters may explain most of the differences in species performance; and 2c) if FD and PD are complementary components of community properties, then we expect that each parameter will explain meaningful fractions of the variability in species performance.

METHODS

Study community and seed collection

We collected seeds of annual plants during May and June in 2019 and 2020, in the following locations in Iberian gypsum steppes of central Spain: Aranjuez (40º02’11.7” N, 3º32’59.5” W; 591 m), Ciempozuelos (40º08’36.9” N, 3º 37’00.0” W, 585 m), Huerta de Valdecarábanos (39°52'37.1"N 3°36'04.3"W, 675 m), Belinchón (40°02'42.8"N 3°03'26.1"W, 732 m), Huete (40°09'08.6"N 2°39'26.6"W, 774 m), and Portalrubio de Guadamejud (40º17’34.4” N, 2º35’31.0” W; 755 m). The climate in these locations is semiarid Mediterranean continental with annual mean precipitations of 365 mm m^{-2} $yr^{-1,}$ concentrated in autumn and early spring, with an intense summer drought. Temperatures range between 33.2°C (July) and 1.2°C (January), from the warmest to coldest months, respectively (Getafe weather station, 40°17'58'' N; 3°43'20'' O; 620 m).

Gypsum soils have characteristics that limit plant life, such as, macronutrient deficiencies (N, P and K) or excess of other nutrients (Ca, Mg and S) (Merlo et al., 2009; Meyer, 1986), high water infiltration and presence and thickness of a hard surface soil crust (Escudero et al., 2015). These systems are dominated by small shrubs that are edaphic specialists, such as *Lepidium subulatum* L., *Centaurea hyssopifolia* Vahl., *Gypsophila struthium* L., *Helianthemum squamatum* (L.) Dum., *Herniaria fruticosa* L., *Thymus lacaitae* Pau, *Teucrium pumilum* Loefl. ex L., and *Frankenia thymifolia* Desf., combined with large plants of *Macrochloa tenacissima* (L.) Kunth. -a tussock forming grass-. Perennial plants develop sparsely distributed patches interspersed in a matrix of biological soil crust mainly composed of lichens and a rich community of annual plants. *Diploschistes diacapsis* (Ach.) Lumbsch, and *Squamarina lentigera* (G.H. Weber) dominate the well-developed biological soil crust (Concostrina-Zubiri et al., 2014), which decisively affect the establishment and development of plants (Ortiz et al., 2023; Peralta et al., 2019; Maestre et al., 2011). The plant community is extraordinarily diverse, with dense seed banks (16.21 seeds/m^2) that can host propagules of up to 68 different species in 0.25 m^2, most of which belong to annual plant species (Caballero et al., 2008, 2003; Peralta et al 2016). The rich regional annual plant species pool is composed by over one hundred taxa (Luzuriaga et al., 2018), with both strict gypsophytes, i.e., species growing preferably on gypsum soils (e.g., *Chaenorhinum reyesii* (C.Vicioso & Pau) Benedí, *Festuca* *gypsicola* (Hack.) Paunero, and *Campanula fastigiata* Dufour ex A. DC), as well as several gypsovags, i.e., species able to grow on gypsum soils as well as on other substrate types (e.g., *Aegilops geniculata* Roth, *Bromus rubens* L., *Galium parisiense* L., *Echinaria capitata* (L.) Desf.), which typically form dense assemblages (e.g., up to 38 species/0.25 m^2 in rainy years (Luzuriaga et al., 2012, 2015). This terophytic community shows two germination peaks (following rainfall events in autumn and spring), and its life cycle extends from October to June, when most annual plant species have dispersed their seeds.

After collection, seeds were cleaned and stored in paper envelopes in a dry environment in the laboratory. Fifteen days before seed sowing (October 2020), seeds were placed in an oven at 50°C to simulate summer conditions and break seed dormancy that would prevent seed germination (Chaves et al., 2021). Seeds were sowed in the surface of pots filled with seed free gypsum soil from a gypsum quarry near the collection sites.

Experimental design

The common garden trial was performed in the CULTIVE facilities at Rey Juan Carlos University (Móstoles, Spain, https://urjc-cultive.webnode.es/) from October 2020 to July 2021. We manipulated the initial phylogenetic diversities in experimental gypsophilous annual plant assemblages by arranging eleven taxonomic combinations from a set of 30 species from the regional pool (Table 1). We created 11 species combinations with contrasting values of initial phylogenetic diversities, ranging from 0.23 to 0.93 in their Phylogenetic Species Variability (PSV) index (Helmus et al., 2007). The PSV is calculated using the formula:

$$PSV = \frac{\mathrm{ntrC} - \sum \mathrm{C}}{\mathrm{n(n-1)}} = 1 - \bar{\mathrm{c}}$$

where C is a covariance matrix reflecting the correlation structure in the phylogeny of the community, trC the sum of the diagonal elements of the covariance matrix C, n the number of species in the community, and $\bar{c}$ represents the mean of diagonal elements of C (Helmus et al., 2007). We calculated PSV based on the phylogenetic tree for the 30 species involved in the experiment (Figure 2). Phylogenetic Species Variability index reflects the degree of phylogenetic relatedness between species in a community (Helmus et al., 2007), ranging between 1 (maximum variability) to 0. Every assemblage contained the same number of species and abundances so, unlike in observational studies, species richness will not affect this index.

Each experimental assemblage consisted in four coexisting species and six individuals per species, simulating natural richness and density values. (Luzuriaga et al., 2012, 2015) relativized by the dimensions of the experimental plots. To this aim, we sowed 20 seeds per species in square pots with 20 x 20 cm width × 21 cm height and 6 L of capacity filled with seed free gypsum soil. We manually removed the excess of emergent seedlings until we got six individuals stablished per species and pot. After adjusting for the phylogenetic diversities, the resulting species combinations were characterized as well in terms of their initial functional diversity based on three key functional traits: (i) specific leaf area (SLA), (ii) seed mass (SM), (iii) maximum plant height (MPH), and (iv) the combination of all traits, with a multi-trait index. The functional traits SLA, SM and MPH were selected as they are considered to estimate critical ecological strategies of the species (Garnier et al., 2016; Westoby, 1998). Functional trait values for 83.3% of our species were obtained from Peralta et al. (2019), the rest of trait values (16.67%) were estimated using *Rphylopars* (Goolsby et al., 2021) on the basis of the information obtained from the phylogenetic tree (Figure 2) built using *phylo.maker* function from the *V.PhyloMaker* package (Jin & Qian, 2019) and the *scenario 1* option to bind new tips. Traits MPH and SM were log transformed prior to statistical analyses to ensure that the data conformed with the assumption of normality (see Figure 2 for the mean trait values of each species).

Functional diversity was measured using Rao's quadratic entropy index (Botta-Dukat, 2005) for each of the functional traits analysed (SLA, SM, and MPH) and for the combination of all traits, in a multi-trait index variable:

$$Rao = \sum \mathrm{d_{ij}}\ \mathrm{p_i p_j}$$

where *i* and *j* represent different species, *d* reflects the distance between i and *j* in terms of the value of a particular functional trait, and *p* represents the proportion of each species in the assemblage. Previously, for the calculation of the multi-trait index variable, we use the following formula:

$$d_{ij} = \frac{1}{n}\sum_{k=1}^{n} x_{ik} - x_{jk}$$

where *n* is the number of traits and x_{ik} represent the value of trait *k* in species *i.*

Rao's quadratic entropy index measures the diversity of a given functional trait in the assemblage by using a multivariate distance measure and allows estimating the distance between species in the ecological niche space (Mason et al., 2005). The value of the Rao index increases when more abundant species have more extreme functional trait values (Mason et al., 2005).

We established 24 pots for each taxonomic combination, half of them received the mean monthly rainfall recorded during 1981-2010 period in the reference station of our study system (Getafe, 40º18'14" N, 3º43'45" O; 622 m) (control irrigation treatment) and the other half received one-third of the mean rainfall for the drought treatment. We used Getafe as the reference weather station because it is the closest one to our seed collection locations recording monthly rainfall data for a series up to 30 years (see Appendix I). We recorded the soil moisture level in two pots per treatment all along the experiment using a time domain reflectometer (model TDR 100, Campbell Scientific, see Appendix II).

Each species combination and irrigation treatment was 12-fold replicated, so we arranged 264 pots (11 taxonomic combination scenarios × 2 irrigation treatments × 12 replicates). From March 2021 to July 2021, we weekly monitored individual plant survival and the number of fruiting plants per pot. In addition, we registered the number of fruits and seeds produced per plant.

Table 1. Complete list of species used in the experiment grouped by the phylogenetic diversity assemblages. The scientific name and family of the species used in each combination are indicated, as well as the value of the Phylogenetic Species Variability index (PSV) and the functional diversity index Rao related to the traits specific leaf area (SLA), seed mass (SM), maximum plant height (MPH) and multi-trait index (combination of SLA, SM and MPH) in each experimental assemblage. The first column corresponds to the letter naming each of the 11 species combinations (A-K).

	Species	Family	PSV	Multi-trait Rao	SLA Rao	SM Rao	MPH Rao
A	*Ctenopsis gypsophila* (Hack.) Paunero *Galium parisiense L.* *Lomelosia stellata* (L.) Raf. *Pistorinia hispanica* (L.) DC	Poaceae Rubiaceae Caprifoliaceae Crassulaceae	0.93	1.25	0.36	0.8	0.09
B	*Bromus rubens L.* *Centaurea melitensis L.* *Galium parisiense L.* *Plantago afra L.*	Poaceae Asteraceae Rubiaceae Plantaginaceae	0.87	1.58	1.01	0.29	0.29
C	*Aegilops geniculata* Roth *Alyssum simplex* Rudolphi *Atractylis humilis L.* *Bombycilaena discolor* (Pers.) M. Laínz	Poaceae Brassicaceae Asteraceae Asteraceae	0.85	2.44	1.06	0.56	0.82
D	*Bombycilaena discolor* (Pers.) M. Laínz *Crepis vesicaria L.* *Echinaria capitata* (L.) Desf. *Malva aegyptia L.*	Asteraceae Asteraceae Poaceae Malvaceae	0.84	1.71	1.17	0.05	0.5
E	*Asteriscus aquaticus* (L.) Less *Bromus rubens L.* *Campanula erinus* L. *Torilis leptophylla* (L.) Rchb.f.	Asteraceae Poaceae Campanulaceae Apiaceae	0.83	2.05	0.63	1.15	0.27
F	*Crepis vesicaria L.* *Lomelosia stellata* (L.) Raf. *Vulpia ciliata* Dumort. *Xeranthemum inapertum* (L.) Mill.	Asteraceae Caprifoliaceae Poaceae Asteraceae	0.77	1.7	0.92	0.65	0.13
G	*Asterolinon linum-stellatum* (L.) Duby. *Cerastium glomeratum* Thuill. *Limonium echioides* (L.) Mill. *Silene conica* (L.)	Primulaceae Caryophyllaceae Plumbaginaceae Caryophyllaceae	0.77	3.4	1.11	0.51	1.78
H	*Cleonia lusitanica* (Loefl. ex L.) L. *Neatostema apulum* (L.) I.M.Jonhston *Plantago afra L.* *Ziziphora hispanica L.*	Lamiaceae Boraginaceae Plantaginaceae Lamiaceae	0.47	0.66	0.18	0.35	0.12

	Species	Family	PSV	Multi-trait Rao	SLA Rao	SM Rao	MPH Rao
I	*Asteriscus aquaticus* (L.) Less	Asteraceae	0.43	3.63	0.99	2.17	0.48
	Campanula erinus L.	Campanulaceae					
	Crupina vulgaris Pers. ex Cass.	Asteraceae					
	Xeranthemum inapertum (L.) Mill.	Asteraceae					
J	*Bupleurum semicompositum L.*	Apiaceae	0.42	1.09	0.19	0.71	0.2
	Lomelosia stellata (L.) Raf.	Caprifoliaceae					
	Scandix L.	Apiaceae					
	Lagoecia cuminoides L.	Apiaceae					
K	*Atractylis humilis L.*	Asteraceae	0.23	2.23	1.48	0.38	0.38
	Bombycilaena discolor (Pers.) M. Laínz	Asteraceae					
	Crepis vesicaria L.	Asteraceae					
	Crupina vulgaris Pers. ex Cass.	Asteraceae					

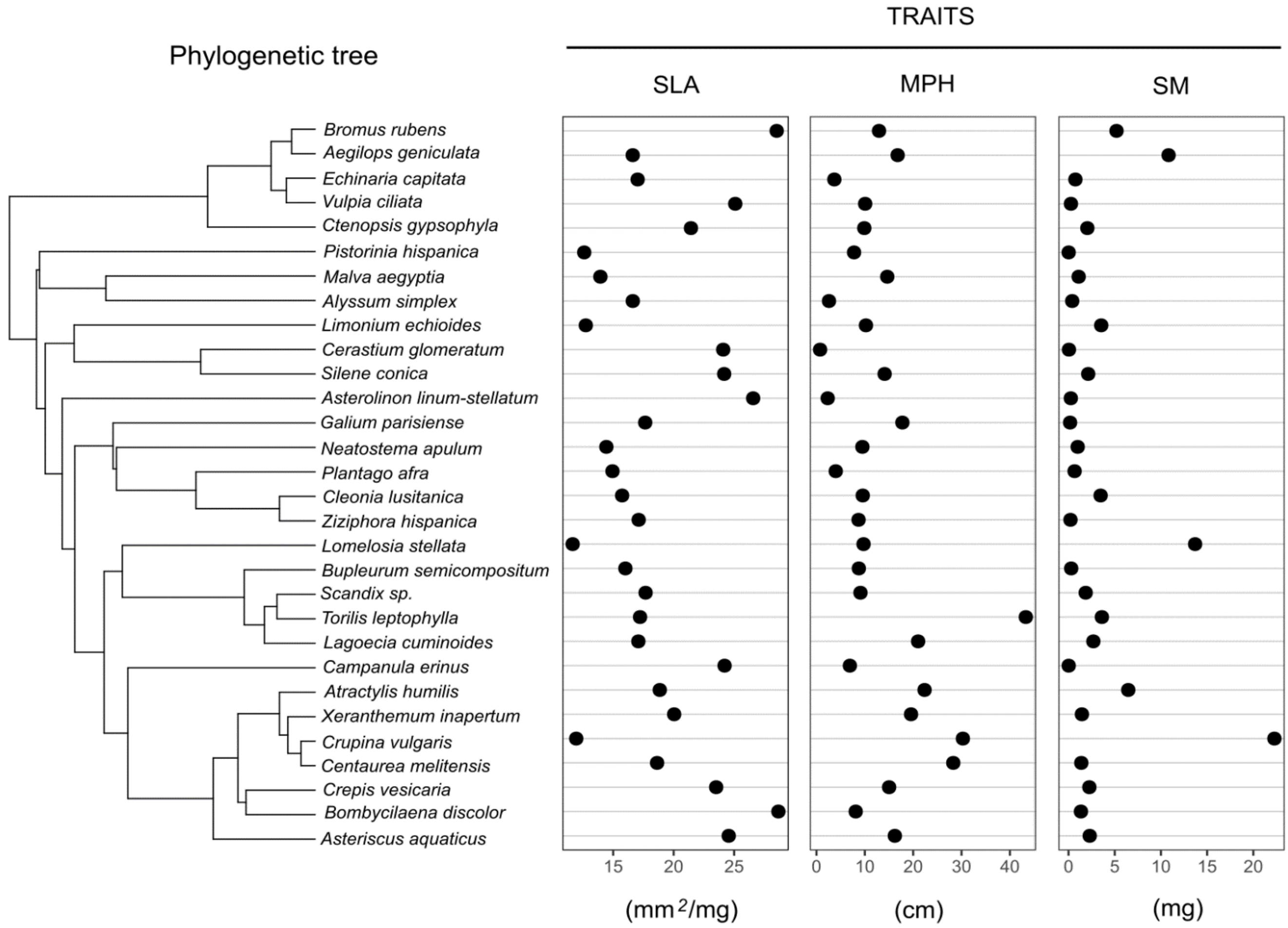


Figure 2. Representation of the phylogenetic tree with the species involved in our experiment accompanied by the values of the functional traits of each species (SLA: specific leaf area, MPH: maximum plant height, and SM: seed mass).

Statistical analyses

To evaluate the likely correlation among phylogenetic and functional diversities of experimental assemblages, we performed Pearson correlations among them (Appendix III). No significant correlation occurred between the initial phylogenetic diversity and the initial functional diversity based on each individual functional trait or on the multi-trait index, however we found significant correlations between the Multi-trait $_{\text{Rao}}$ index with MPH $_{\text{Rao}}$ (R=0.7, p=0.016) and with SLA $_{\text{Rao}}$. (R=0.64, p=0.035).

Plant survival

Species survival was estimated as the proportion of surviving individuals per species in each pot at each sampling date. Generalized linear mixed models (GLMMs) were used to analyse the effect of the initial phylogenetic diversity and initial functional diversity using the four functional indices in independent statistical models (SLA $_{\text{Rao}}$, MPH $_{\text{Rao}}$, SM $_{\text{Rao}}$ and Multi-trait $_{\text{Rao}}$) combined with water availability conditions on the dependent variable (proportion of surviving individuals). We included the terms pot identity and species identity as random factors. Irrigation treatment was included as a fixed factor, and the initial phylogenetic and the functional diversity were considered as covariates, including their interactions. sampling time was also considered as a covariate. Thus, we performed four complementary models, each one including the initial functional diversity associated to SLA, SM, MPH, and the multi-trait index, respectively. Since the response variable is expressed as a proportion (values from 0 to 1), we used the Binomial distribution family and the logit link function.

Reproductive success

We measured the reproductive success of each species in two ways: (a) At the species level: the final proportion of fruiting plants related to the initial number of plants of each species per pot; (b) At the individual level: the average number of seeds per plant produced by each species per pot. This variable was standardized as follows:

$$Z = \frac{x_i - \mu}{\sigma}$$

Where μ is the mean number of seeds produced per species in our study and σ the standard deviation. In order to make this variable positive to perform GLMMs, the most negative value per species was added to all values.

We performed GLMMs to analyse the effect of initial phylogenetic and functional diversities of each species assemblage combined with water availability treatment on each dependent variable (proportion of fructified plants and average number of seeds per plant). We included the term species identity as a random factor. Irrigation treatment was included as a fixed factor, initial phylogenetic and functional diversities as covariates and all their interactions were considered. We performed four complementary models, using the functional diversity based on one of the three functional traits studied (SLA, SM and MPH), and based on the multi-trait index. At the species level since the response variable is a proportion, we used the Binomial distribution and the logit link function and at the individual level, we used the Gaussian distribution and the identity link function.

We used the *glmer* function of the *lme4* package (Bates et al., 2015) to perform GLMMs. To calculate Rao indices, we used the *dbFD* function of the *FD* package (Laliberté et al., 2014; Laliberté & Legendre, 2010), and packages *ape* (Paradis & Schliep, 2019) and *picante* (Kembel et al., 2010) to calculate phylogenetic indices. We use the package *ggplot2* to create all the figures (Wickham, 2016). All analyses were performed with the R software version 4.0.5 (R Core Team, 2021).

RESULTS

Our results evidenced that high phylogenetic diversity in species assemblages increased fruiting plant proportion and seed production of coexisting species even after statistically controlling for the variability explained by the initial functional diversity based separately on the three key functional traits and on the multi-trait index, and completed their life cycles in a shorter time lapse than in less diverse ones (Tables 2 and 3; Figure 3, 4 and 5).

Table 2. Generalized linear mixed models (GLMMs) for the proportion of surviving plants per species and pot. Pot and species identities were considered as random factors, irrigation treatment (W) as a fixed factor, the initial phylogenetic diversity (PSV), initial functional diversity (Rao), and weeks since the beginning of the experiment (Time) as covariates, the interaction terms between all variables were included. Phylogenetic diversity was measured as the PSV (Phylogenetic Species Variability) index and functional diversity as Rao's quadratic entropy (Rao's) index calculated for each of the three functional traits: specific leaf area (SLA), seed mass (SM), and maximum plant height (MPH), and for multi-trait response. Functional diversity based on each of the three functional traits and for multi-trait response were considered in independent models. The chi-square values (χ^2) after calculating type III errors are shown: ***p<0.001; **p<0.01; *p<0.05; †p<0.1.

Proportion of surviving plants
per species and pot
(n=19008)

		Multi-Trait	SLA	SM	MPH
	Df	χ^2	χ^2	χ^2	χ^2
(Intercept)	1	8.98 **	9.15 **	9.05 **	10.78 **
Time	1	**18145.28 *** **	**18148.17 *** **	**18145.15 *** **	**18146.21 *** **
Phylogenetic diversity (PSV)	1	2.15	**4.07 * **	**5.26 * **	0.02
Irrigation treatment (W)	1	**605.24*** **	**620.29 *** **	**610.21 *** **	**602.33 *** **
Rao	1	1.32	**15.67*** **	**5.13* **	1.14
PSV x W	1	**16.12 *** **	**16.76 *** **	**15.31 *** **	**14.89*** **
PSV x Rao	1	**5.87 * **	**4.88 * **	0.10	**7.99 ** **
W x Rao	1	1.69	**11.71 *** **	0.32	1.17

Table 3. Generalized linear mixed model (GLMMs) for: (a) the final proportion of fruiting plants related to the initial number of plants of each species per pot; (b) the average number of seeds produced by each fruiting plant per species per pot. We considered irrigation treatment (W) as a fixed factor, the initial phylogenetic diversity (PSV), initial functional diversity (Rao) as covariates, and interactions between variables were included. We included the terms pot identity and species identity as random factors for proportion of fruiting plants (a) and only pot identity for average number of seeds (b) analyses. Phylogenetic diversity was measured as the PSV (Phylogenetic Species Variability) index and functional diversity as Rao's quadratic entropy (Rao's) index calculated for each of the three functional traits: (a) specific leaf area (SLA), (b) seed weight (SM), and (c) maximum plant height (MPH) and for the multi-trait index. Each of the three functional traits and for multi-trait response was included separately in each model. The chi-square values (χ^2) after calculating type III errors are shown.: ***p<0.001; **p<0.01; *p<0.05; †p<0.1.

a)

		Proportion of fruiting plants per species and pot (n=1031)			
		Multi-Trait	SLA	SM	MPH
	Df	χ^2	χ^2	χ^2	χ^2
(Intercept)	1	53.45 ***	58.96 ***	79.1 ***	51.51 ***
Phylogenetic diversity (PSV)	1	**(+) 12.51 *****	2.46	**(+) 18.91 *****	**(+) 45.26 *****
Irrigation treatment (W)	1	**1308.75 *****	**1277.12 *****	**1284.03 *****	**1309.91 *****
Rao	1	**(+) 30.67 *****	**(-) 9.71** **	**(+) 13.68 *****	**(-) 28.11 *****
PSV x W	1	**(+) 9.58 ****	**(+) 18.77** ***	3.83 †	**(+) 11.95** ***
PSV x Rao	1	**(+) 62.73 *****	**(+) 64.58 *****	0.00	**(+) 61.07 *****
W x Rao	1	0.003	**(+) 24.34 *****	**(-) 22.61 *****	**(+) 3.86** *

b)

		Average number of seeds per plant per species and pot (n=711)			
		Multi-Trait	**SLA**	**SM**	**MPH**
	Df	χ^2	χ^2	χ^2	χ^2
(Intercept)	1	4198.89 ***	4216.37 ***	4026.95 ***	3226.81 ***
Phylogenetic diversity (PSV)	1	0.73	0.14	0.84	2.99 †
Irrigation treatment (W)	1	**668.57 *** **	**672.57 *** **	**670.21 *** **	**670.06 *** **
Rao	1	0.62	0.01	0.22	1.02
PSV x W	1	**(-) 25.74 *** **	**(-) 23.52 *** **	**(-) 20.25 *** **	**(-) 27.79 *** **
PSV x Rao	1	2.7	**(-) 4.56** *	0.02	3.48 †
W x Rao	1	1.43	**(-) 5.06** *	**(+) 4.74** *	3.03 †

In average irrigation treatments, most annual plant species were able to successfully complete life cycles (i.e., more than the 75% of individuals of each species produced fruits), independently of the initial phylogenetic and functional diversities (Figures 4 and 5). In addition, in the phylogenetically more diverse neighbourhoods, plants completed their life cycles in a shorter time lapse than in less diverse ones, as we can observe in the shorter time lapse until annual plants died following fruit production (Figure 3). Remarkedly, in drought treatments, species growing in phylogenetically diverse neighbourhoods had a higher proportion of fruiting plants than those growing in neighbourhoods composed of closer relatives (Figure 4 and 5). Specifically, when including the functional diversity of MPH, SLA and the multi-trait index in the models, a significant interaction occurred between the initial phylogenetic and functional diversities on the proportion of plant survival and of fruiting plants per species (Tables 2 and 3a). In these cases, the proportion of fruiting plants per species increased with the functional diversity until a certain threshold, where it decreased forming a unimodal trend (Figure 4). Each fruiting plant produced more seeds in more diverse neighbourhoods specially under drought conditions (Table 3b; Figure 5).

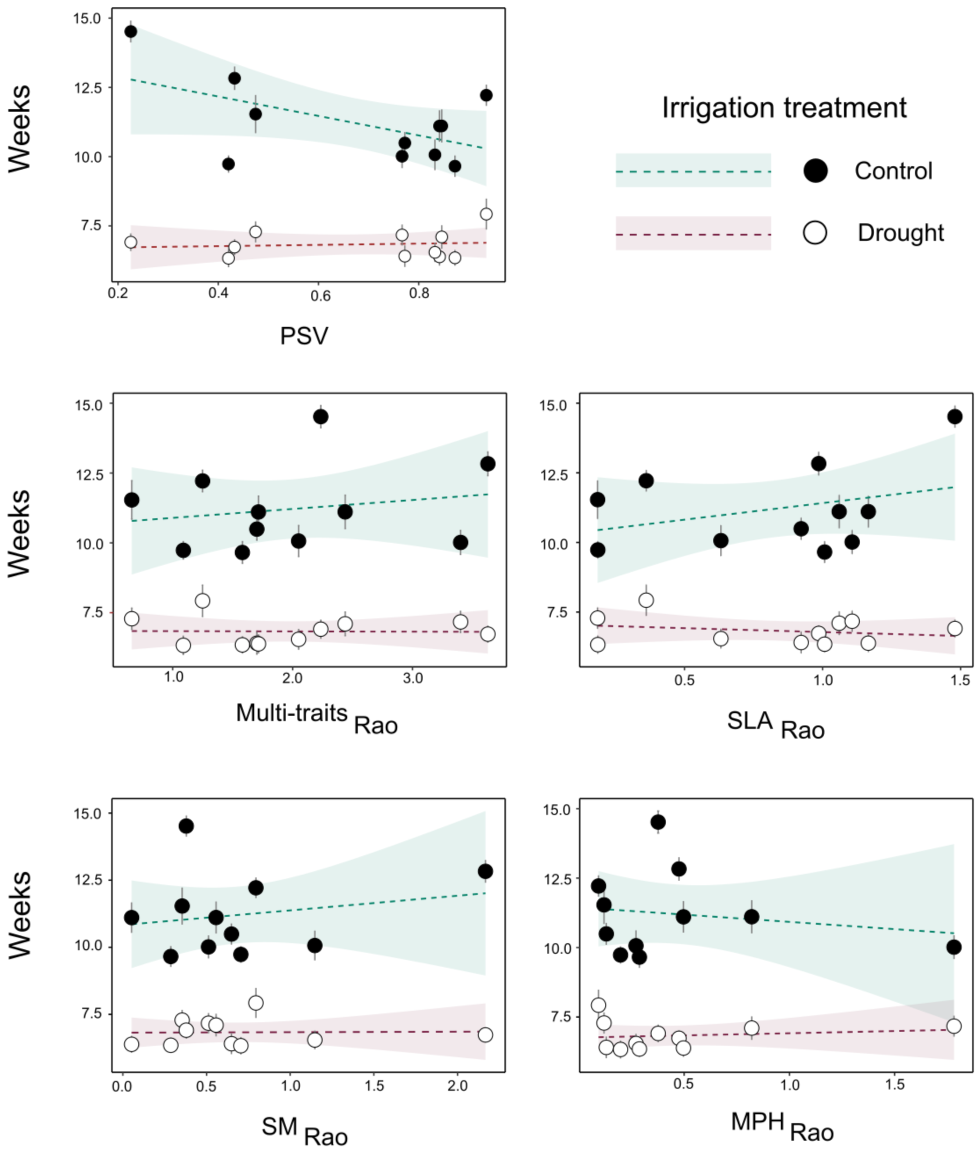


Figure 3. Average time length (in weeks) elapsed until plant survival becomes 50% of initial individuals (t50) in each species combination conforming the experimental assemblages(i.e., 11 taxonomic combinations), represented as a function of: a) initial phylogenetic diversity (PSV); b) initial functional diversity measured with multi-trait response (Multi-traits $_{\text{Rao}}$) using the key functional traits specific leaf area (SLA), seed mass (SM) and maximum plant height (MPH); c) initial functional diversity measured with the Rao index of SLA; d) initial functional diversity measured with the Rao index SM; and e) initial functional diversity measured with the Rao index of MPH. Bold and empty symbols correspond to control and drought irrigation treatments, respectively. Bars represent the standard error of the average t50 per species combination and treatment, and shading areas are the confidence intervals.

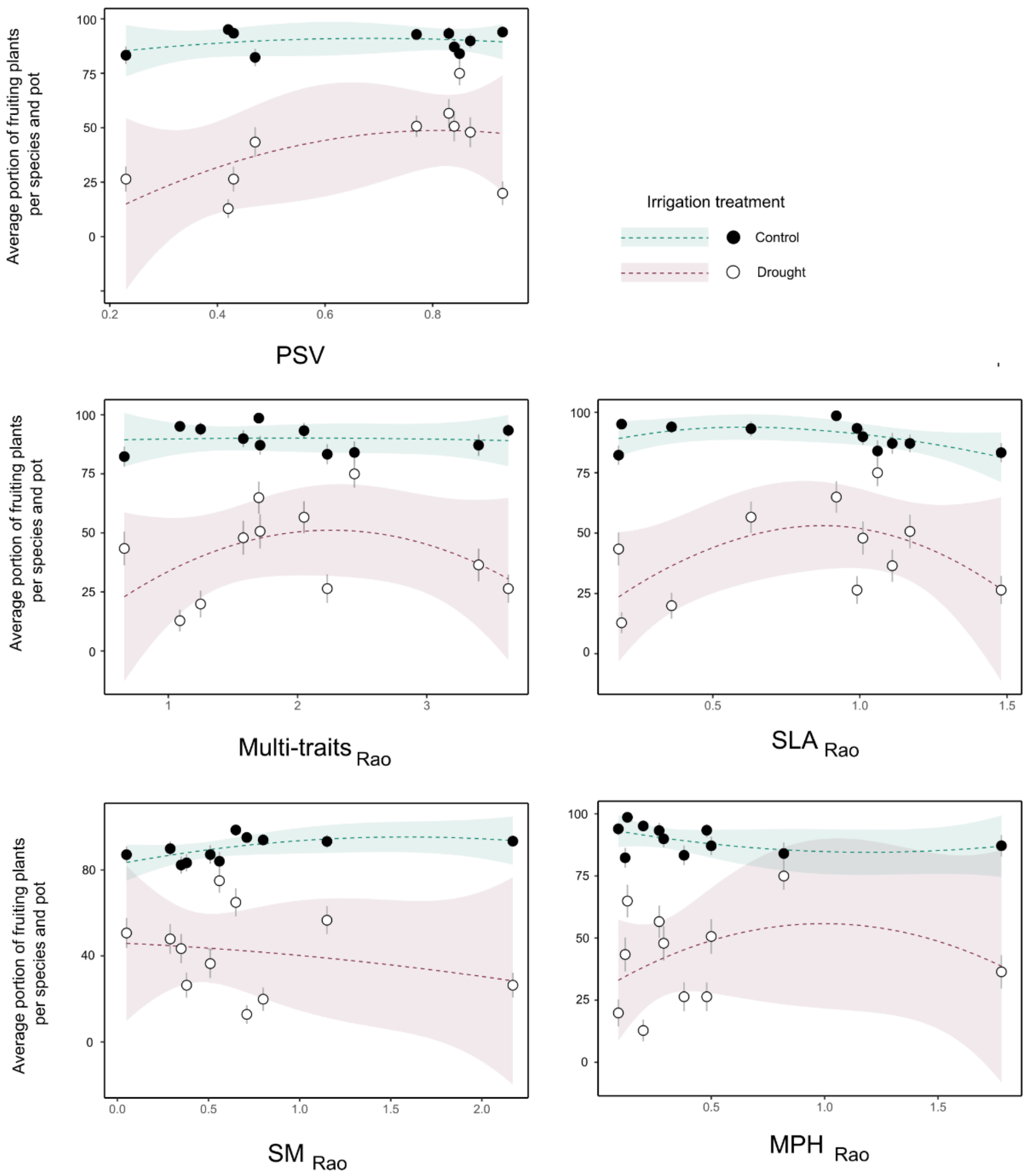


Figure 4. Average proportion of fruiting plants per species and pot in each species combination conforming the experimental assemblages (i.e., 11 taxonomic combinations), recorded as a function of: a) initial phylogenetic diversity (PSV); b) initial functional diversity measured with multi-trait response (Multi-traits $_{\text{Rao}}$) using the key functional traits specific leaf area (SLA), seed mass (SM) and maximum plant height (MPH); c) initial functional diversity measured by the Rao index of SLA; d) initial functional diversity measured by the Rao index of SM; and e) initial functional diversity measured by the Rao index of MPH. Bold and empty symbols correspond to control and drought irrigation treatments, respectively. Bars represent the standard error of the average portion of fruiting plants per species and pot and treatment, and shading areas are the confidence intervals.

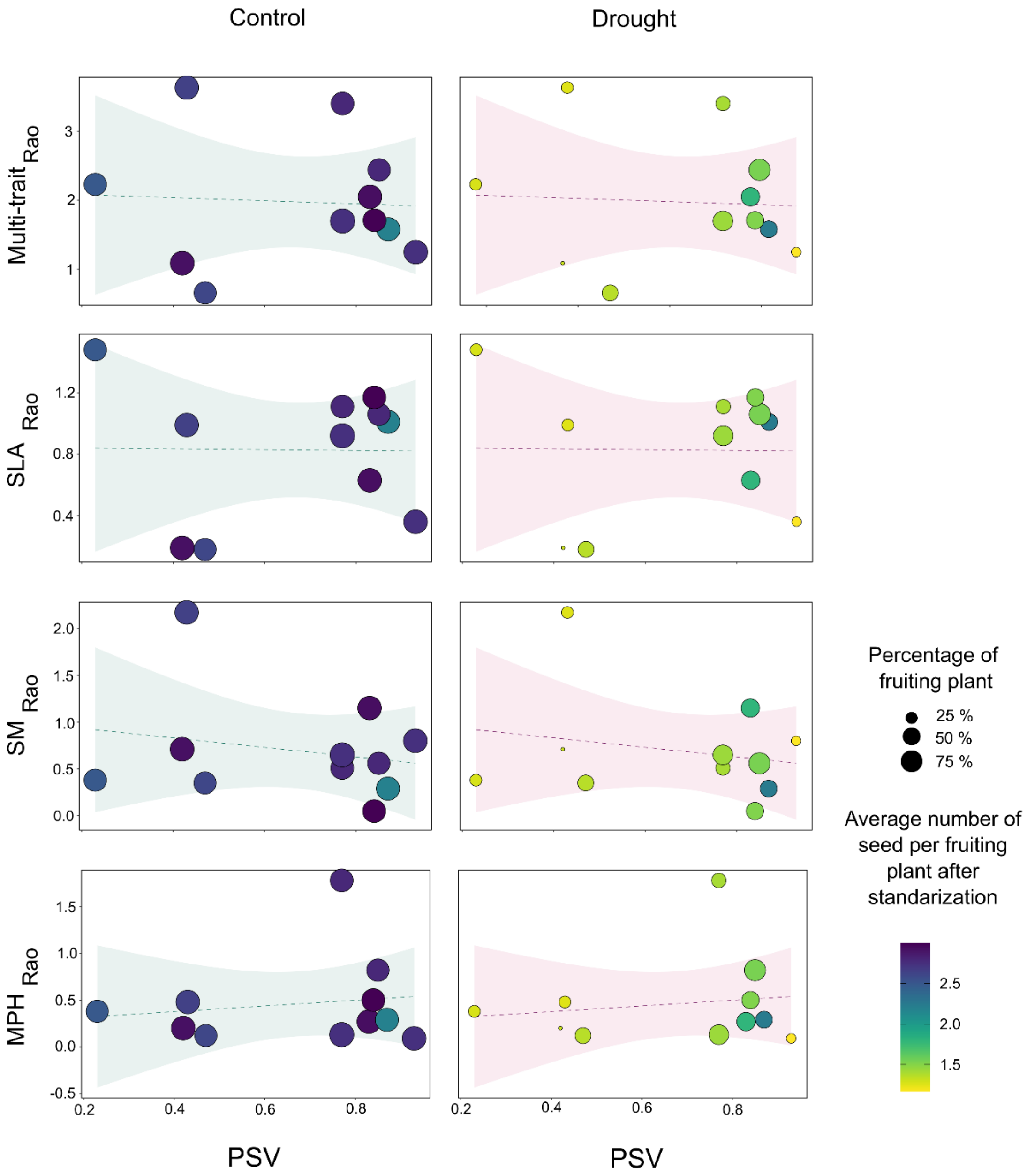


Figure 5. The final percentage of fruiting plants per species and pot (represented by the circle size) and the average number of seeds produced per each fruiting plant per species and pot after standardization (represented by the colour gradient), as a function of the irrigation treatment (control: in the left side; drought: in the right side) and the initial phylogenetic and functional diversities for specific leaf area (SLA), seed weight (SM),and maximum plant height (MPH) and the multi-trait diversity index.

DISCUSSION

In this study, we demonstrated that phylogenetic and functional diversities of the community affected the performance of coexisting annual plants. Our results confirmed that the initial phylogenetic diversity of species assemblages is a crucial driver of community level processes (see also Chaves et al., 2021). Furthermore, the effect of the phylogenetically diverse neighbourhoods on species performance goes beyond the likely effect of functional diversity of three main functional traits of plants (SM, MPH and SLA) and even when considering the multi-trait functional diversity index combining the three traits. Thus, regardless of the effect of the functional diversity on the coexisting species performance, we still detected a powerful effect of the phylogenetic diversity of the species neighbourhoods on the performance of its components.

In response to our first question, in phylogenetically diverse assemblages, a higher proportion of plants fructified and even produced more seeds than in phylogenetically less diverse ones. This result confirms our hypothesis that phylogenetic relationships between species predict the niche requirements of the component species (Hypothesis 1a, Figure 1a). These results, reinforce the idea previously demonstrated by Chaves et al. (2021), supporting that phylogenetic diversity reflects the diversity of ecological roles (Muñoz et al., 2017) of coexisting species. Concretely, our results support that niche complementarity is associated with phylogenetic diversity (Srivastava et al., 2012; Fargione et al., 2007; Webb et al., 2002). The performance of plants improves with greater phylogenetic diversity, which means greater niche complementarity, favouring less competition between species. Thus, these species would invest more resources in reproduction. Phylogenetically more distant species tend to have more differences in their morphophysiological and phenotypical characteristics (Kraft et al., 2014) and, therefore, they may differ more in their resource use strategies, so they are more likely to coexist due to the attenuation in the intensity of competition between them (Silvertown, 2004). Although previous studies have already explored this idea (see Chaves et al., 2021; López-Angulo et al., 2018), with this study we extend the range of initial phylogenetic diversity values, and we included three traits' values of each participant species.

Following the niche conservatism theory (Wiens et al., 2010), species more related are more similar, whereas more distant species are less similar and therefore, present more complementary niches (Staab et al., 2021). Therefore, evolutionary divergence may explain biotic niche differences (Srivastava et al., 2012; Webb et al., 2002), so if we assume that traits are phylogenetically conserved (Burns & Strauss, 2011; Cavender-Bares et al., 2009; Furniss et al., 2017; Purschke et al., 2017) then phylogenetic diversity resume the functional differences between species (Staab et al., 2021). Functional diversity measured as the combination of the three traits (multi-trait diversity index) explained a significant portion of variability, independent of that explained by phylogenetic diversity in one of the two fitness variables (proportion of fructified plants) and is also consistent with the hypothesis that multi-trait functional distances between species reflect niche differences (Kraft et al., 2015). Therefore, we can affirm that the main mechanism determining annual plant communities in the semi-arid is niche complementarity, according to studies that corroborated that assemblages with distantly related species contributed most to the higher biomass production in multispecies assemblages, through species complementarity (Engbersen et al., 2022; Cadotte, 2013; Cavender-Bares et al., 2004). However, when we analysed the effect of functional diversity based on individual traits, we observed that they explained significant fractions of the proportion of fruiting plants independent of the effect of the initial phylogenetic diversity. For example, when diversity of SLA and MPH in the assemblage is higher, a smaller number of plants fructified. SLA and MPH traits are known to predict plant competitive ability, consequently large differences in SLA (and MPH) between species may be reflecting competitive asymmetry among coexisting species (Pacala & Weiner, 1991). Therefore, in our study system, competition, specifically competitive asymmetry, is also modulating communities as has been demonstrated in other semi-arid regions of the planet (Ben-Hur & Kadmon, 2015; García-Camacho et al., 2017). On the other hand, higher diversity in SM_{Rao} was associated with a higher proportion of fruiting plants. This result supports that differences in SM would predict differences in species niche requirements favouring niche complementarity. If we focus on the small spatial scale, large differences in SM mean large differences in seedling and root sizes of coexisting species in the early stages of assembly. These different sized seedlings are less likely to compete among different species because they capture resources from different soil depth strata. This would explain why higher differences in seed size, at least during the early performing stages, promote niche complementarity and favour more individuals to fructify.

During the last few years, functional and phylogenetic diversities have been used as proxies to explain community assemblage (Langenheder et al., 2012; Flynn et al., 2011; Graham & Fine, 2008; Kraft et al., 2011; Meynard et al., 2011; Mouchet et al., 2010). Recent studies, as Galland et al. (2019), suggested that phylogenetic and functional diversities offer complementarity information to explain community resistance to natural colonization in an experiment adding seeds in field plots. However, in pairwise species experiments Godoy et al (2014) found that phylogenetic relatedness among species is not always associated to the intensity of competitive interactions, even when niche-related traits or competitive ability are conserved across the phylogeny. Instead, other studies (Cadotte et al., 2019), support that phylogenetic diversity and functional diversity offer complementary information, phylogenetic diversity reflected better multivariate conserved ecological features, while single traits better captured recent divergence between species.

In short, the results of this study suggest that the initial phylogenetic diversity of annual plant assemblages could be a good predictor of plant survival and reproductive success. Niche complementarity and competitive asymmetry are neither contradictory nor exclusive but help us to better understand what is happening in our communities. Niche complementarity acts as a mechanism that allows multiple species to coexist, which would explain why our environments are so species-rich even though competition between annual plants has also been demonstrated. Niche complementarity avoids competitive forces between coexisting species, as it allows species to persist that would otherwise end up excluding each other through competition. Furthermore, the effect of individual interactions (neighbourhood exclusion), observed at small spatial scales (Webb et al., 2002), also influence traits and evolutionary processes in a feedback loop between ecological and evolutionary processes (sensu Cavender-Bares et al., 2009). In this study, functional diversity was significant once we statistically controlled for phylogenetic diversity. While phylogenetic diversity probably integrates the entire evolutionary history of species, the extra variability that explains functional diversity, using the multi-trait index, is probably related to more recent evolutionary changes. Phylogeny is a good proxy to the ecological niche of species, as it seems to summarise the morphological, physiological and phenological characteristics throughout the evolution of species and it integrates plant responses to environmental conditions. Therefore, annual plant communities in Iberian semi-arid gypsiferous systems seem to be strongly organised around competitive relationships, which would make niche complementarity one of the central mechanisms of assembly under water stress conditions. In this context, higher phylogenetic diversity in the assemblages will favour plant success.

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Supporting information

CHAPTER 4

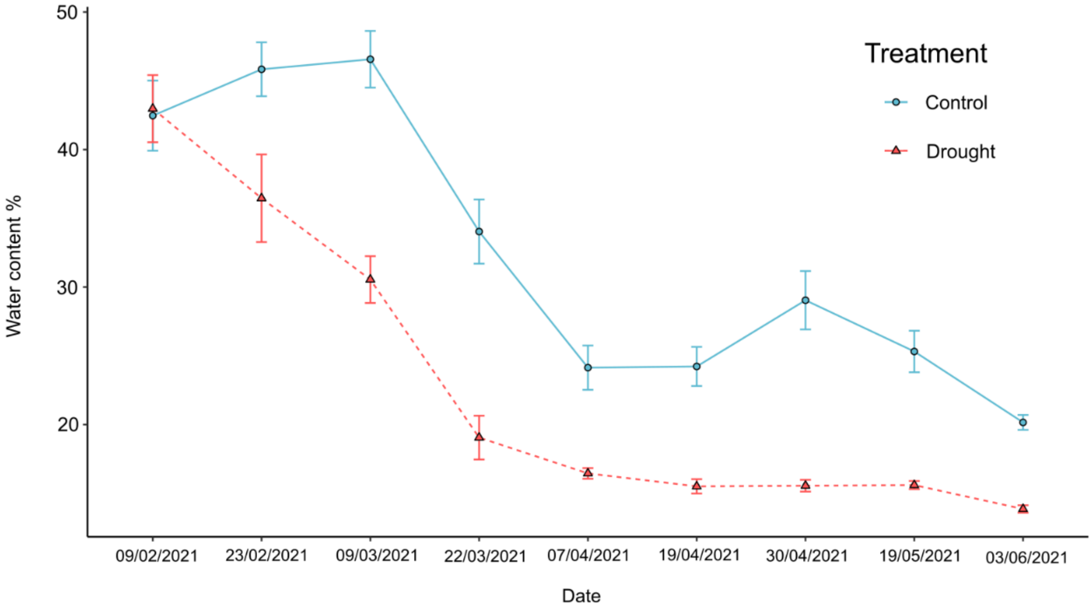
Phylogenetic and functional diversities offer complementary information to disentangle species assembly processes in experimental gypsophilous annual plant assemblages.

Laura Ortiz, Pablo Ferrandis, Laura Rodríguez and Arantzazu L. Luzuriaga

Appendix I. Table summarising the amount of water received each month in each phylogenetic diversity scenario. The information on precipitation is taken from the Getafe station (40°17'58'' N; 3°43'20'' O; 620 m), which provides the mean precipitation registered over 30 years (1981 - 2010).

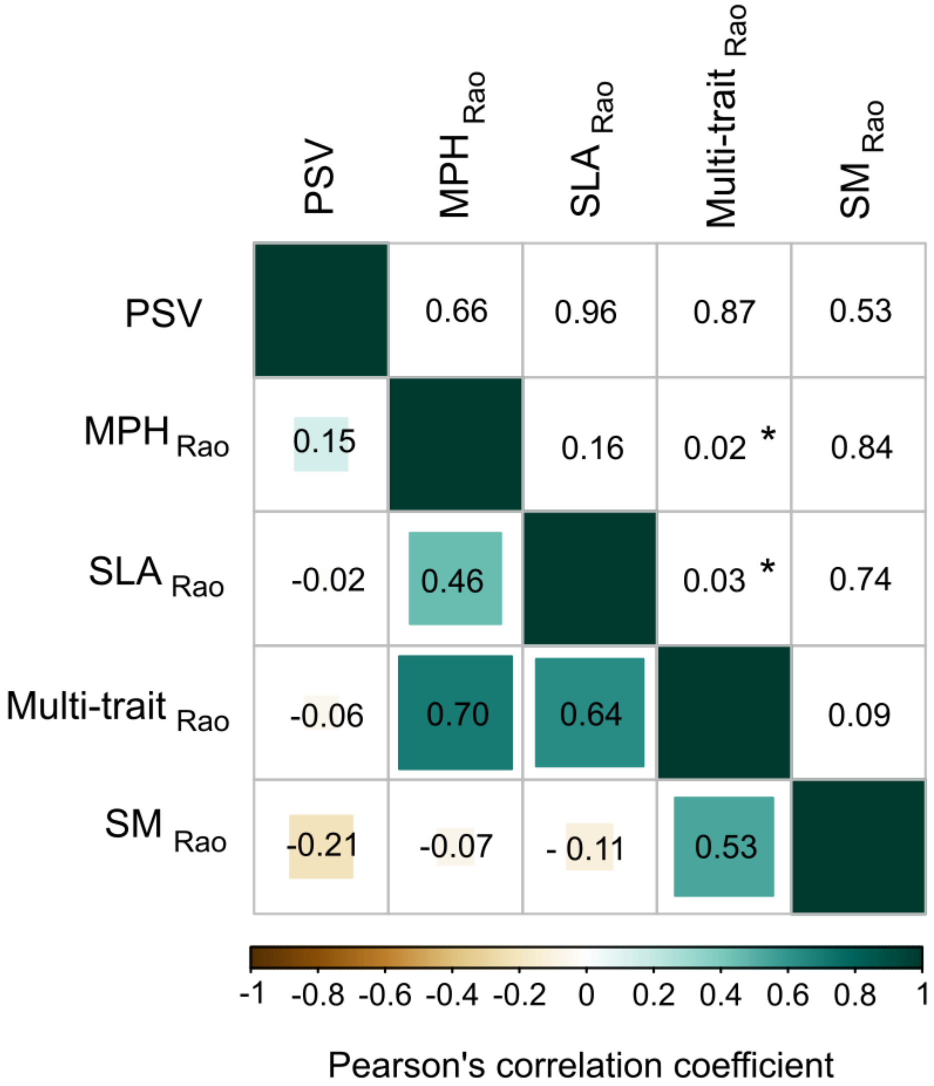
				Amount of irrigation	
Month	**Mean precipitation** (mm)	**Monthly irrigation** (litres/pot)	**Days of irrigation per month**	**Control treatment** (litres/pot)	**Drought treatment** (litres/pot)
October	50	2	8	0.25	0.075
November	48	1.92	8	0.24	0.072
December	45	1.8	8	0.22	0.067
January	30	1.2	8	0.15	0.045
February	32	1.28	8	0.16	0.048
March	24	0.96	9	0.11	0.032
April	38	1.52	8	0.19	0.057
May	39	1.56	8	0.19	0.059
June	19	0.76	8	0.09	0.028
July	9	0.36	8	0.04	0.013

Appendix II. Mean values of the soil water content in pots in the irrigation control and drought treatments (n= 22 in all cases) recorded during the experiment, measured by using a time domain reflectometry (TDR) method. Vertical bars represent standard errors.



		Date								
Pot	Treatment	9-Feb	23-Feb	9-Mar	22-Mar	7-Apr	19-Apr	30-Apr	19-May	3-Jun
A1R-2	Control	0.47	0.46	0.76	0.19	0.21	0.26	0.20	0.24	0.20
A1R-10	Control	0.35	0.48	0.58	0.20	0.19	0.20	0.24	0.20	0.20
A1N-3	Drought	0.26	0.20	0.27	0.17	0.18	0.18	0.17	0.15	0.15
A1N-7	Drought	0.56	0.51	0.21	0.18	0.18	0.16	0.17	0.17	0.15
A2R-1	Control	0.46	0.47	0.51	0.41	0.22	0.24	0.29	0.21	0.20
A2R-6	Control	0.40	0.39	0.44	0.24	0.20	0.20	0.21	0.23	0.19
A2N-5	Drought	0.46	0.26	0.24	0.17	0.16	0.15	0.15	0.15	0.12
A2N-11	Drought	0.46	0.40	0.24	0.14	0.15	0.23	0.13	0.16	0.13
A3R-3	Control	0.47	0.45	0.40	0.38	0.20	0.31	0.45	0.23	0.19
A3R-12	Control	0.51	0.40	0.47	0.21	0.20	0.20	0.37	0.28	0.20
A3N-4	Drought	0.29	0.20	0.29	0.13	0.12	0.11	0.11	0.13	0.12
A3N-9	Drought	0.47	0.41	0.39	0.18	0.17	0.15	0.15	0.14	0.14
A5R-6	Control	0.50	0.51	0.52	0.44	0.21	0.21	0.42	0.25	0.20
A5R-12	Control	0.65	0.60	0.34	0.44	0.44	0.35	0.20	0.19	0.20
A5N-3	Drought	0.45	0.43	0.30	0.19	0.17	0.16	0.16	0.16	0.15
A5N-7	Drought	0.39	0.22	0.38	0.17	0.14	0.12	0.20	0.13	0.13
A6R-1	Control	0.47	0.48	0.36	0.45	0.33	0.37	0.42	0.30	0.22
A6R-5	Control	0.61	0.56	0.38	0.48	0.21	0.21	0.21	0.24	0.21
A6N-3	Drought	0.36	0.21	0.32	0.16	0.16	0.16	0.15	0.17	0.14
A6N-6	Drought	0.47	0.55	0.30	0.20	0.18	0.15	0.16	0.16	0.14
A7R-2	Control	0.45	0.23	0.40	0.20	0.18	0.22	0.23	0.20	0.19
A7R-10	Control	0.20	0.28	0.41	0.43	0.32	0.27	0.40	0.39	0.19
A7N-5	Drought	0.34	0.23	0.23	0.17	0.16	0.16	0.16	0.16	0.15
A7N-9	Drought	0.46	0.27	0.23	0.17	0.19	0.16	0.16	0.16	0.14
B1R-4	Control	0.22	0.45	0.46	0.41	0.22	0.20	0.21	0.28	0.20
B1R-7	Control	0.42	0.45	0.38	0.40	0.21	0.17	0.18	0.18	0.19
B1N-5	Drought	0.35	0.20	0.28	0.16	0.18	0.15	0.15	0.16	0.13
B1N-9	Drought	0.61	0.64	0.30	0.43	0.17	0.16	0.18	0.15	0.14
B2R-2	Control	0.30	0.48	0.50	0.39	0.20	0.21	0.20	0.21	0.19
B2R-8	Control	0.44	0.37	0.47	0.42	0.19	0.22	0.18	0.20	0.26
B2N-7	Drought	0.44	0.39	0.29	0.16	0.15	0.13	0.13	0.14	0.12
B2N-12	Drought	0.65	0.68	0.58	0.40	0.19	0.19	0.19	0.18	0.17
B3R-2	Control	0.40	0.46	0.48	0.21	0.21	0.21	0.39	0.21	0.19
B3R-8	Control	0.36	0.54	0.39	0.46	0.22	0.33	0.43	0.37	0.20
B3N-6	Drought	0.42	0.31	0.36	0.16	0.15	0.14	0.14	0.14	0.13
B3N-11	Drought	0.57	0.50	0.35	0.18	0.19	0.15	0.16	0.17	0.14
B5R-7	Control	0.62	0.64	0.63	0.45	0.43	0.39	0.39	0.44	0.28
B5R-11	Control	0.36	0.44	0.48	0.22	0.33	0.20	0.36	0.20	0.19
B5N-4	Drought	0.28	0.32	0.35	0.15	0.14	0.13	0.13	0.15	0.13
B5N-8	Drought	0.51	0.45	0.30	0.18	0.18	0.16	0.17	0.16	0.15
B7R-4	Control	0.45	0.48	0.47	0.19	0.19	0.19	0.22	0.33	0.17
B7R-9	Control	0.24	0.47	0.40	0.29	0.20	0.17	0.19	0.18	0.17
B7N-6	Drought	0.20	0.19	0.21	0.14	0.14	0.14	0.14	0.16	0.13
B7N-10	Drought	0.44	0.44	0.28	0.22	0.16	0.16	0.16	0.18	0.16

Appendix III. Pearson correlation between the initial phylogenetic diversity (measured from the PSV index, Phylogenetic Species Variability) and the initial functional diversity (from Rao's quadratic entropy index) of three functional traits: i) specific leaf area (SLA), ii) seed weight (SM), iii) maximum plant height (MPH) and multi-trait index. The size of the square represents the Pearson's correlation coefficient, measured as a ratio of 0 to 1, and the colour indicates the sign of the correlation, also insight the square is the exact value of Pearson's correlation coefficient. In the upper diagonal, each quadrat has the p-value of Pearson correlation, significative values are marked with an asterisk *.



	PSV	MPH_{Rao}	SLA_{Rao}	$\text{Multi-trait}_{\text{Rao}}$	SM_{Rao}
PSV		0.66	0.96	0.87	0.53
MPH_{Rao}	0.15		0.16	0.02 *	0.84
SLA_{Rao}	-0.02	0.46		0.03 *	0.74
$\text{Multi-trait}_{\text{Rao}}$	-0.06	0.70	0.64		0.09
SM_{Rao}	-0.21	-0.07	- 0.11	0.53	

DISCUSIÓN GENERAL

DISCUSIÓN GENERAL

Este trabajo nos ha permitido conocer mejor los procesos de ensamblaje y coexistencia de la comunidad dominada por plantas anuales que encontramos en el sistema semiárido yesífero del centro de la Península Ibérica. Nuestros resultados confirman que, durante años con precipitaciones igual o superiores a la media, los procesos estocásticos predominaron frente a los procesos deterministas en el ensamblaje de nuestra comunidad (Capítulo 1). Confirmamos, además, que la llegada de propágulos tiene una especial relevancia en el ensamblaje de estas comunidades (Capítulos 1 y 2) y que los microambientes que crean los factores bióticos (presencia de *Macrochloa tenacissima* y costra biológica del suelo -CBS- en este caso), influyen en la formación de las comunidades de plantas (Capítulos 1, 2 y 3). La presencia de *M. tenacissima* no tiene un claro efecto facilitador, además, su parte subterránea (parte radicular) parece competir por los recursos (Capítulo 2). Por otra parte, la presencia de CBS actúa en un primer momento como filtro físico dificultando la entrada de algunas especies, pero las que consiguen establecerse se benefician de la mejora de las condiciones por parte de la CBS traduciéndose en un mayor crecimiento y fitness (mayor número de frutos producidos por planta) (Capítulo 3). Los efectos producidos por parte de estos componentes bióticos parecen estar precedidos por la variabilidad climática interanual que actuaría como un primer filtro de especies (Capítulos 1 y 2). Además, complementariamente a los experimentos observacionales, hemos desarrollado novedosos experimentos de jardín común en los que manipulamos toda la comunidad de plantas anuales. Esto nos ha permitido explorar los efectos causales de las propiedades filogenéticas y funcionales de la comunidad sobre la supervivencia, el establecimiento y el fitness de las especies vegetales coexistentes, lo que finalmente puede determinar los mecanismos de ensamblaje (Capítulos 3 y 4).

Procesos estocásticos vs. procesos deterministas

Los resultados que obtuvimos con el experimento de campo que desarrollamos durante cuatro años (Capítulo 1) nos reveló cómo los procesos estocásticos estuvieron muy activos en la formación de nuevos ensambles, especialmente en los años que se produjeron precipitaciones cercanas a la media histórica (2021) o años especialmente húmedos (2020 y 2022). Bajo estas condiciones, no detectamos ningún filtrado de rasgos funcionales asociados a microambientes específicos, en nuestro caso asociados a la presencia de *Macrochloa tenacissima* y CBS. Esto nos indica que el filtrado determinista no parece desempeñar un papel destacado, al menos en estas primeras fases de recuperación de los ensamblajes, donde el ensamblaje de especies se produjo de manera aleatoria, independientemente del componente biótico. Probablemente, las condiciones climáticas fueron lo suficientemente favorables para que las especies del pool regional se establecieran y completaran sus ciclos vitales. Estas especies han evolucionado para hacer frente a condiciones aún más restrictivas y, en consecuencia, prevalecieron los procesos estocásticos dando lugar a ensamblajes aleatorios. La misma tendencia estocástica en la formación de comunidades se ha visto en estudios en ambientes más favorables (Chase & Myers, 2011; Chase, 2010; Volkov et al., 2007; Latimer et al., 2005; Condit et al., 2002). Con todo ello, podemos afirmar que, aunque las especies presentan diferenciación de nicho y rasgos funcionales, tales diferencias pudieron ser de menor importancia para los procesos de ensamblaje de especies en años con precipitaciones medias y años húmedos (Holt, 2006). Este estudio es la primera prueba que demuestra que, en los sistemas semiáridos de yesos, la estocasticidad podría ser un impulsor importante de los procesos de ensamblaje durante años con condiciones favorables para estas plantas.

Por otro lado, aunque los factores ambientales no generaron una clara selección de especies basada en sus rasgos, sí que afectaron al porcentaje de cobertura vegetal y a la diversidad taxonómica (Capítulos 1 y 2). La presencia de CBS aumentó tanto el porcentaje de cobertura vegetal como la diversidad taxonómica, mientras que en presencia de *M. tenacissima* se redujeron. Probablemente, los componentes bióticos modificaron las condiciones microambientales pero no hasta el extremo de desencadenar interacciones competitivas entre especies coexistentes. Por tanto, cabría esperar que prevalezca la estocasticidad, ya que, en entornos más favorables sin una competencia significativa entre especies, cualquier especie presente en el banco de semillas del suelo podría, potencialmente, tener éxito. Además, la importancia relativa de los procesos neutros, probablemente, disminuya con el aumento del estrés ambiental (Qiao et al., 2015), como se ha comprobado en estudios en nuestra comunidad de plantas anuales frente a un estrés hídrico muy marcado (Peralta et al., 2023; 2019). En definitiva, debemos tener en cuenta tanto la teoría del nicho (Chase & Leibold, 2003) como la teoría de la neutralidad (Rosindell et al., 2011; Hubbell, 2001) para comprender los mecanismos tanto de ensamblaje como de coexistencia (Qiao et al., 2015; Weiher et al., 2011; Vellend, 2010; Vergnon et al., 2009; Alonso et al., 2006; Holt, 2006; Pacala & Tilman, 1994). Ya que, como hemos comprobado con nuestros experimentos (Capítulo 1 y 2), aunque la estocasticidad dominara sobre los procesos deterministas, los componentes bióticos también intervinieron en la formación de nuestra comunidad, por ejemplo, en presencia de CBS aumentó la riqueza de especies y el porcentaje de cobertura vegetal, y lapresencia de *M. tenacissima* modificó la composición de especies.

Efecto de la variabilidad climática interanual

La variabilidad climática interanual que caracteriza los sistemas Mediterráneos semiáridos (Blondel et al., 2010) propicia que la precipitación varíe cada año, por lo que nuestras comunidades dominadas por plantas anuales hacen frente cada año a una disponibilidad hídrica diferente. Además, la marcada variabilidad interanual de las precipitaciones modula la estacionalidad y la cantidad de agua disponible cada año (Vargas-Colin et al., 2022; Luzuriaga et al., 2012, 2015).

Aunque estas variaciones climáticas son frecuentes en nuestro sistema, y por tanto los episodios de sequía también, durante el desarrollo de los experimentos de campo, el primero con una duración de 4 años y el segundo de 3 (Capítulo 1 y 2) solo experimentamos un año con valores de precipitación por debajo de la media (2019). A excepción del año 2019, el resto de los años, las precipitaciones durante el periodo de desarrollo vegetal (septiembre – mayo) fueron iguales o superiores a la media de referencia en nuestro sistema de estudio (1981 – 2010).Las comunidades de plantas anuales de sistemas semiáridos parecen estar adaptadas a esta variabilidad climática (Tielbörger et al., 2014) y en los años en los que las condiciones son más favorables aprovechan para establecerse. Además, estas comunidades son muy resilientes y un solo año con alta disponibilidad de agua permite la recuperación taxonómica y funcional de los ensamblajes de especies tras varios años secos (López-Rubio et al., 2022). Por tanto, la variabilidad climática interanual juega un papel clave induciendo escenarios de ensamblaje alternativos con diferentes combinaciones funcionales (Violle et al., 2017). Previos estudios en nuestro sistema (Sánchez et al., 2022; Peralta et al., 2019) ya habían comprobado la importancia de la cantidad y la estacionalidad de las precipitaciones en la formación de las comunidades vegetales anuales, detectando selección de rasgos cuando el estrés hídrico era muy fuerte, concretamente, cuando el tratamiento de riego reducía la cantidad de agua a un tercio de la precipitación media en la zona de estudio.

Complementariamente, en el capítulo 4 hemos controlado la disponibilidad de agua estableciendo dos escenarios (riego promedio y sequía). Con estos tratamientos comprobamos como en condiciones de riego promedio, la mayoría de las especies (más del 75 %) fueron capaces de completar con éxito sus ciclos vitales. Esto confirma una vez más que cuando las condiciones son propicias, nuestras especies tienen la capacidad tanto de establecerse como de completar su ciclo vital con éxito, es decir, logran producir frutos y semillas de manera exitosa.

Con nuestros resultados todo indica a que la disponibilidad hídrica actúa como un primer filtro ambiental, seleccionando las especies que mejor puedan adaptarse a las condiciones de estrés hídrico del momento y determinando así el conjunto de especies disponibles para el ensamblaje de la comunidad vegetal (Luzuriaga et al., 2012). Confirmando además la idea de que la cantidad de agua disponible en el suelo determina, en gran medida, la estructura de las comunidades vegetales en ambientes semiáridos (Chesson et al., 2004; Miranda et al., 2011).

Efecto de la disponibilidad de propágulos en el suelo

El modelo de Dinámica en Espiral (Caballero,et al., 2008) explica la estrecha relación entre la vegetación presente en el suelo y el banco de semillas en los sistemas semiáridos. Es decir, la vegetación que encontramos en un determinado espacio produce semillas que van a parar al suelo cercano formando el banco de semillas, a su vez este banco de semillas es el que determinará la vegetación que se establezca al año siguiente. Este proceso se repetirá año tras año resultando en que la composición de especies que observamos en la vegetación aérea y los bancos de semillas del suelo tiendan a estar altamente correlacionados (López-Rubio et al., *in preparation*; Peralta et al., 2016; Martinez-Duro et al., 2012; Caballero et al., 2008a; 2008b; Olano et al., 2005). En nuestros experimentos en campo (Capítulos 1 y 2) comprobamos la importancia de la disponibilidad de propágulos en el suelo para la formación de las comunidades vegetales de sistemas semiáridos.

Sorprendentemente, tras cuatro años, la vegetación aérea que se desarrolló en los suelos con presencia de semillas no se igualó a la vegetación aérea en los suelos sin semillas (Capítulo 1 y 2). Este resultado es contrario a lo que esperábamos, basándonos en estudios anteriores (Escudero et al., 2015; Martinez-Duro et al., 2012; Olano et al., 2012) que indicaban una rápida recuperación del banco de semillas. Después de 4 años de seguimiento las parcelas con suelo inicial libre de semillas no se igualaron ni en riqueza de especies ni en porcentaje de cobertura total de plantas con el suelo que presentaba el banco de semillas natural, previamente homogeneizado para asegurarnos la completa disponibilidad de semillas (Capítulo 1). Además, obtuvimos los mismos resultados en los tratamientos en los que relajamos el filtrado abiótico inicial mediante la adición de agua (tratamiento de riego, Capítulo 2). Estos resultados podrían estar indicándonos que la llegada de semillas no es tan masiva como se pensaba (Martínez-Duro et al., 2009, 2010). Tanto la riqueza, como la homogeneidad que presentan los bancos de semillas de estas comunidades (Martinez-Duro et al., 2012; Olano et al., 2012) podrían ser el resultado de la producción de semillas durante muchas generaciones que se han acumulado en el suelo en las proximidades a las plantas madre debido a la corta distancia de dispersión que presentan estas especies (Peralta et al., 2023, 2016: López-Rubio et al., *in preparation;* Olano et al., 2012) debido, en el caso de las plantas anuales, a su pequeña altura principalmente y a que la mayoría carecen de estructuras especializadas de dispersión (Ellner & Shmida, 1981; Venable et al., 2008). Además, las semillas de especies anuales pueden permanecer en el banco de semillas en estado latente en lugar de germinar para minimizar el riesgo de una situación de estrés, estrategia conocida como "bet-hedging" (Venable, 2007). Por lo tanto, aunque la llegada y trasiego de semillas no fue muy relevante en nuestro sistema, debemos remarcar que la disponibilidad de semillas en el suelo fue determinante en la formación de las comunidades de plantas anuales.

Efecto de la presencia de *Macrochloa tenacissima*

La facilitación que se produce entre una planta nodriza y las plantas que se establecen a su alrededor está considerado un factor clave en el desarrollo de las comunidades que viven en ambientes estresantes como los sistemas semiáridos (Brooker et al., 2008; Michalet et al., 2006; Bertness & Callaway, 1994; Madrigal-González et al., 2020; Filazzola & Lortie, 2014; Luzuriaga et al., 2012). Además, según la Hipótesis del Gradiente de Estrés (Bertness & Callaway, 1994), la facilitación predominaría sobre la competencia en condiciones de estrés. Por todo ello, cabría esperar que la presencia de *M. tenacissima* actuara como planta nodriza, ejerciendo un papel facilitador en nuestro sistema (Madrigal-González et al., 2020; Luzuriaga et al., 2012; Maestre et al., 2007; 2001). Sin embargo, al contrario de lo que apuntaban estudios previos (Pugnaire et al., 2011; Maestre et al., 2007; Maestre et al.,2001) en nuestros experimentos de campo (Capítulo 1 y 2) no hemos detectado ningún efecto facilitador de esta especie sobre las comunidades de plantas anuales.

Con el primer experimento de campo (Capítulo 1), comprobamos cómo, contrariamente a lo que esperábamos, las plantas de *M. tenacissima* no favorecieron la retención de semillas bajo su dosel durante los eventos de dispersión primaria y secundaria de semillas (Bullock & Moy, 2004). En el segundo experimento (Capítulo 2) nos centramos en estudiar, por separado, el efecto de las partes aéreas y subterráneas del esparto para ver el papel que juegan en el establecimiento de la comunidad. Con este experimento observamos que la parte subterránea, el sistema radicular de *M. tenacissima* parece competir con las especies que se establecen próximas. Probablemente se produzca una competencia directa por el agua entre el esparto y las especies que se establecen a su alrededor (Armas & Pugnaire, 2011) debido a que la cantidad de agua que consumen las plantas de *M. tenacissima* es mayor que el agua recibida (Maestre et al., 2003). Por otro lado, la parte aérea de las plantas que no estaban activas no resultaron en un aumento de la riqueza ni la cobertura vegetal total, por lo que parece estar produciéndose un efecto de sombra seca (Valladares et al., 2004,2001). Este efecto consiste en que la sequía pueda ser más intensa a la sombra producida por el esparto al competir por los recursos y producirse un mayor estrés hídrico. Solamente, en escenarios en los que, mediante el tratamiento de riego, rebajamos el estrés hídrico, observamos un efecto positivo de la parte aérea del esparto en la riqueza y cobertura de las comunidades de anuales, pero únicamente en el suelo libre de semillas. En definitiva, y contrastando con la idea extendida de que la presencia de *M. tenacissima* puede mejorar tanto la supervivencia como la diversidad de especies, ya que mejora las condiciones microambientales de la zona en la que se establecían (Maestre et al., 2007; Maestre & Cortina, 2005; Maestre et al., 2001). Nuestros resultados muestran un efecto generalmente negativo de la presencia de *M. tenacissima* sobre las comunidades de plantas anuales.

Efecto de la presencia de costra biológica del suelo

La presencia de costra biológica del suelo (CBS), dominada por líquenes en nuestro sistema, afectó a la formación de la comunidad al intervenir de manera significativa en todas las etapas del ciclo de vida de nuestras especies. La heterogeneidad creada por la presencia de CBS en el suelo favoreció una mayor riqueza de especies y cobertura en las comunidades que partían de suelos libres de semillas (Capítulo 1), probablemente porque intervino como trampa para las semillas que se dispersaron en el entorno. La CBS también influyó en el establecimiento y posterior desarrollo de nuestra comunidad de plantas anuales (Capítulos 1 y 3). Confirmamos con nuestros resultados, la relevancia de esta capa biótica del suelo en el desarrollo de las comunidades de plantas anuales gipsófilas del centro peninsular.

La estructura física creada en el suelo por la presencia de CBS actuó como trampa para semillas, atrapándolas en su movimiento horizontal (Bowker et al., 2018; Zhang et al., 2016), este reclutamiento en combinación con la mejora de las condiciones microambientales bajo su influencia (Boeken, 2008; Belnap, 2003) contribuyó a la rápida recuperación de los ensamblajes de especies y por ende a los bancos de semillas del suelo (Capítulo 1). Este resultado es importante, debido a que sólo ante la presencia de CBS, se igualaron la riqueza taxonómica, la diversidad y la composición de especies en los suelos homogeneizados naturales y suelos sin semillas solamente un año después de la puesta en marcha del experimento (Capítulo 1).

En el primer experimento de jardín común que realizamos en el invernadero (Capítulo 3) comprobamos el efecto que la presencia y estructura de CBS tiene a lo largo del ciclo vital de las especies anuales, desde su establecimiento a su posterior desarrollo. La presencia de CBS restringe el establecimiento de las especies anuales debido a que forma una gruesa capa física muy difícil de traspasar por algunas especies (Escudero et al., 2007; Meyer, 1986; Romão & Escudero, 2005). Aunque con nuestro diseño experimental no podemos descartar las propiedades alelopáticas que probablemente presenta la CBS (Tay et al., 2004), sí que podemos confirmar que la restricción física es un factor importante en el establecimiento de las especies anuales. Ya que, en presencia de CBS intacta, sobre todo, pero también cuando la CBS aparecía perturbada, la proporción de plantas que germinaron fue menor que en las macetas en las que no había presencia de CBS. Sin embargo, una vez que consiguen establecerse parecen beneficiarse de las condiciones creadas por la presencia de la CBS y mejoran tanto su crecimiento como su reproducción (producción de mayor número de frutos). Además, esta respuesta de las plantas anuales a la presencia de CBS estuvo modulada por la diversidad funcional de las comunidades creadas (Ortiz et al., 2023), como veremos más adelante.

Diversidad funcional: efectos y causas

En los dos experimentos de campo (Capítulos 1 y 2) hemos identificado el efecto de los tratamientos experimentales sobre la estructura funcional de las especies en las comunidades resultantes. Hemos seleccionado seis rasgos funcionales porque recogen las estrategias ecológicas fundamentales vinculadas al desarrollo de las plantas y a la formación de comunidades (Cornelissen et al., 2003; Westoby, 1998). Estos rasgos son: área foliar específica (SLA); contenido de materia seca foliar (LDMC); la relación entre la masa seca subterránea / masa seca aérea, (root:shoot ratio); la proporción de masa seca reproductiva/vegetativa (rep/veg); la altura máxima de la planta (MPH) y la masa de las semillas (SM).

En el primer experimento (Capítulo 1), esto nos ha permitido comprender el reemplazo de las características dominantes de las especies que se establecen a lo largo del desarrollo de la comunidad a partir de suelos homogeneizados y suelos libres de semillas. Las especies que primero se establecieron en nuestra comunidad presentaron altos valores de SLA, rep/veg y LDMC y bajos valores de proporción raíz/tallo, y en los años posteriores los valores de SLA, rep/reg y LDMC disminuyeron y aumentaron los valores de la proporción raíz/tallo. Todo ello nos sugiere que las especies pioneras, que suelen contar con hojas muy productivas y una baja inversión en raíces, fueron las primeras en establecerse para dar paso los siguientes años a especies más conservadoras. Esto evidenciaría que las especies que llegan tienen más probabilidades de establecerse cuando sus rasgos funcionales les permiten hacer frente a las condiciones iniciales más restrictivas (Galland et al., 2019; Thuiller et al., 2009), de acuerdo con las teorías de complementariedad de nicho y a la Teoría de la Limitación de la Similitud (MacArthur & Levins, 1967).

Aunque, generalmente, no observamos una clara selección de rasgos por parte de los componentes bióticos estudiados, sí que observamos cambios en los valores de ciertos rasgos en presencia de esparto. En el capítulo 2, observamos que la relajación del filtrado abiótico (mediante el tratamiento de riego) incrementó los valores de SLA de las comunidades, sin embargo, en presencia de plantas de *M. tenacissima* intactas los valores de SLA se redujeron. Esto sería otra prueba de cómo el esparto ejerce una intensa competencia radicular, podrían estar seleccionando especies con bajo SLA adaptadas a condiciones de sequía en los ensamblajes próximos. Además, en zonas abiertas, sin presencia de esparto, las especies presentaron un menor porte (valores menores de MPH) que las especies que se desarrollaron bajo la presencia de plantas intactas de *M. tenacissima*. Probablemente las especies más altas aumentan sus probabilidades de competir por los recursos y sobrevivir bajo la presencia de esparto.

Como anticipamos previamente, la respuesta de las plantas anuales a la presencia de CBS estuvo modulada por la diversidad funcional de las comunidades creadas (Ortiz et al., 2023). Uno de los aspectos más novedosos del capítulo 3 es la creación de comunidades manipulando su diversidad funcional inicial, es decir, seleccionando las especies que van a formar parte de la comunidad en base a un determinado rasgo. En nuestro caso hemos seleccionado la altura máxima de la planta (MPH) porque estudios previos demostraron que el MPH es un rasgo funcional particularmente sensible al filtrado de la CBS (Peralta et al., 2019), siendo las plantas anuales de gran tamaño más exitosas en el establecimiento cuando la CBS permanecía intacta, y porque la altura de las plantas nos aporta información significativa sobre la capacidad competitiva por la luz que se establece entre las plantas (Garnier et al., 2016; Westoby et al., 2002; King, 1990). Para este experimento, creamos combinaciones de especies con valores altos de MPH (plantas grandes), con valores bajos de MPH (plantas pequeñas) y mezclando especies con valores altos y bajos de MPH (plantas grandes y pequeñas). Este novedoso enfoque nos ha permitido comprobar cómo la diversidad funcional de los ensambles asociada a un solo rasgo como el MPH contribuye a determinar el desarrollo de las especies. Cuando la diversidad funcional fue mayor, observamos que la producción de frutos de muchas de las especies también aumentó. Esto podría deberse a la influencia de la complementariedad de nichos sobre la organización de nuestra comunidad, ya que las comunidades que presentaban mayores diferencias en sus alturas (mayor diversidad funcional) serían capaces de amortiguar la competencia por los recursos entre ellas. Esta amortiguación podría deberse a la mitigación de la competencia por diferencias de estatura, que además puede favorecer un llenado más eficiente del espacio tanto en la superficie como distribuyéndose para ocupar y tomar recursos de diferentes capas del suelo (Pacala & Levin, 1997). De esta manera estas plantas invertirían más en la producción de frutos que las plantas que comparten vecindario con individuos con alturas parecidas.

Por otro lado, en el capítulo 4, en el que contábamos con ensambles de especies que presentaban inicialmente diferentes valores iniciales de diversidad funcional, encontramos que cuando la diversidad de SM en los ensambles fue mayor, se produjo un aumento en el número de plantas que fructificó. Grandes diferencias en el tamaño de semillas suelen significar grandes diferencias en el tamaño de las plántulas y de las raíces de las especies coexistentes (Garnier et al., 2016; Moles & Leishman, 2008). Como ya hemos apuntado, plántulas de distinto tamaño parecen amortiguar la disputa por los recursos entre especies diferentes porque capturan recursos de estratos de profundidad del suelo diferentes.

Diversidad filogenética: causa y efectos

En nuestro estudio manipulando la diversidad filogenética inicial (Capítulo 4) comprobamos como, en los ensamblajes más diversos filogenéticamente, bajo condiciones de estrés hídrico, la proporción de plantas que fructificó y el número de semillas que produjeron fue mayor que en ensambles con menor diversidad filogenética. Estos resultados apoyan la idea de que la complementariedad de nicho está asociada a la diversidad filogenética (Fargione et al., 2007; Srivastava et al., 2012; Webb et al., 2002), es decir, las relaciones filogenéticas entre especies predicen los requerimientos de nicho de las especies que conforman la comunidad. En un estudio en esta misma línea (Chaves et al., 2021) ya demostraron que la diversidad filogenética reflejaba la diversidad de roles ecológico (Muñoz et al., 2017) de la comunidad. Si tenemos en cuenta que, las especies más distantes filogenéticamente tienden a presentar mayores diferencias, tanto morfológicas como características fenotípicas (Kraft et al., 2014) podemos esperar que presenten diferentes estrategias a la hora de conseguir recursos. Lo que se traduciría en una atenuación de la competencia (Silvertown, 2004) y una mayor complementariedad de nicho (Staab et al., 2021; Wiens et al., 2010). Como apuntábamos, previos estudios ya habían explorado esta idea (Chaves et al., 2021; López-Angulo et al., 2018) pero con este estudio hemos aumentado el rango de diversidad filogenética. Además, hemos introducido la diversidad funcional medida utilizando tres rasgos funcionales importantes (SM, SLA y MPH) y también la combinación de los tres rasgos (índice multifuncional) ya que el uso de un índice multifuncional parece explicar mejor las diferencias de nicho (Kraft et al., 2015) ya que abarcan las principales estrategias ecológicas críticas de las especies (Garnier et al., 2016; Westoby, 1998).

Son muchos los estudios que durante los últimos años han utilizado tanto la diversidad funcional como filogenética para explicar los procesos que intervienen en el ensamblaje de comunidades (Flynn et al., 2011; Graham & Fine, 2008; Kraft, 2011; Langenheder et al., 2012; Meynard et al., 2011; Mouchet et al., 2010). Nuestros resultados se ajustan a la propuesta de Cadotte et al. (2019) que defiende que la diversidad filogenética y la funcional ofrecen información complementaria. Mientras que la diversidad filogenética reflejaría mejor los rasgos ecológicos conservados, desde una perspectiva multifuncional los rasgos individuales capturarían mejor la divergencia reciente entre especies.

Mecanismos de ensamblaje

Con todo ello podemos concluir que el proceso que predomina en el ensamblaje de las comunidades dominadas por plantas anuales del centro peninsular, en año con precipitaciones iguales o superiores a la media, es la estocasticidad. Además, la complementariedad de nicho parece ser el mecanismo que permite la coexistencia de especies en un ambiente con una riqueza de especies muy elevada (Engbersen et al., 2022; Cadotte, 2013; Cavender-Bares et al., 2004), sin que ello signifique que otros mecanismos como la competencia o la facilitación intervengan en la formación de la comunidad. Destacando, además, la importancia de las características funcionales de la comunidad a la hora de activar estos diferentes mecanismos de coexistencia y de la diversidad filogenética a la hora de predecir estas interacciones.

La complementariedad de nicho es un mecanismo que actúa permitiendo la coexistencia de múltiples especies. En nuestro sistema, explicaría por qué son comunidades tan ricas en especies, aunque se haya demostrado la competencia que surge entre plantas anuales (Ben-Hur & Kadmon, 2015; García-Camacho et al., 2017). La complementariedad de nicho controla la competencia entre especies coexistentes, ya que permite que coexistan especies que, de otro modo, acabarían excluyéndose por competencia entre ellas. En nuestro estudio, hemos comprobado esta complementariedad de nicho cuando a mayor diversidad de tamaño máximo de las plantas (escenarios con valores diversos de MPH, Capítulo 3) la producción de frutos de las especies que coexisten en esos ensambles fue mayor. Esto nos demuestra de que las comunidades que presentan especies con gran variabilidad de tamaños máximos evitarían la competencia entre ellas, pudiendo así invertir más energía en la producción de frutos. También observamos (Capítulo 4) como en los ensamblajes filogenéticamente más diversos, una mayor proporción de plantas fructificó e incluso produjo más semillas por fruto que en los filogenéticamente menos diversos. Como ya hemos apuntado, las especies filogenéticamente más distantes suelen presentar más diferencias en sus características morfofisiológicas y fenotípicas (Kraft, Net al., 2014) lo que implica una mayor diferencia en las estrategias que tiene para conseguir y utilizar los recursos. Por lo tanto, es más probable que especies más alejadas filogenéticamente coexistan debido a la atenuación en la intensidad de la competencia entre ellas (Silvertown, 2004). Todo ello encajaría con lo que propone Chaves et al. (2021) de que la complementariedad de nicho puede mitigar la intensidad competitiva entre plantas vecinas, siendo un importante mecanismo de ensamblaje en la naturaleza.

A su vez, la competencia, concretamente la asimetría competitiva, también está modulando las comunidades, como se ha demostrado en otras regiones semiáridas del planeta (Ben-Hur & Kadmon, 2015; García-Camacho et al., 2017). Estas especies tan efímeras presentan ciclos de vida altamente sincronizados (Luzuriaga et al., 2012) lo que propicia una explosión de vida cuando las condiciones son las adecuadas. Hemos observado mecanismos de competencia en escenarios donde todas las plantas tenían un tamaño parecido (ensambles con especies solo de bajo porte o solo de alto porte, Capítulo 3). En este caso, las especies presentaban una capacidad competitiva similar, al tener tamaños parecidos, lo que las hacía invertir más en crecimiento que en producción de frutos. Dentro del rango de plasticidad de cada especie, estas invirtieron más en crecimiento para superar o igualar a sus vecinas en la carrera por la luz. La complementariedad de nicho y la asimetría competitiva no son contradictorias ni excluyentes, sino procesos que pueden estar ocurriendo simultáneamente en una comunidad entre diferentes grupos de especies que coexisten y que nos ayudan a comprender mejor lo que ocurre en nuestras comunidades.

Otros mecanismos que intervienen en la formación de la comunidad son los mecanismos de facilitación, que en este estudio hemos comprobado con la presencia de CBS y de esparto (Capítulos 2 y 3). Si bien es cierto que el efecto facilitador de la CBS (Capítulo 3) lo apreciamos una vez establecidas las plantas, es decir en su etapa de desarrollo y reproducción, ya que en la primera etapa de establecimiento actúa de barrera física. Por otro lado, solamente hemos encontrado facilitación por parte del esparto con la sombra que proporciona su parte aérea, en suelos sin presencia previa de semillas y en condiciones de relajación del filtro abiótico (tratamiento de riego), por lo que no podemos generalizar que el esparto actúe como planta nodriza en la formación de nuestras comunidades (Capítulo 2).

Limitaciones y futuras líneas de investigación

Aunque en nuestro estudio hemos incluido seis rasgos funcionales, que pensamos resumen las características más importantes de las plantas y con las que se pueden explicar los diferentes procesos de establecimiento y reproducción, es cierto que, debido a la complejidad de todos los aspectos de la fisiología de una planta, cuantos más rasgos incluyamos mejor podremos explicar que está sucediendo. Uno de los aspectos que no hemos podido explorar tanto como nos hubiera gustado es la parte radicular de las plantas. Recientes estudios han comprobado como la riqueza de especies, composición y distribución espacial son diferentes en la parte aérea y en la parte subterránea de una comunidad (Illuminati et al., 2021). Comprender mejor la parte radicular de la comunidad, no solo nos ayudará a entender mejor la diversidad de estrategias de uso del agua por las especies coexistentes en zonas áridas (Illuminati et al., 2022; de La Puente et al., 2022), también parece factible que una mayor diversidad de tamaños de plantas pueda contribuir también a mitigar la intensidad competitiva a través de mecanismos de partición de nicho promovidos por un uso más eficiente del espacio (Pacala y Levins 1997) como resultado de la distribución de las raíces a lo largo de las diferentes capas del suelo. Aunque se están haciendo grandes avances para conocer la importancia de los rasgos asociados a las raíces (Funk et al., 2021), la dificultad para medir los rasgos radiculares mantiene una laguna que, sin embargo, requeriría atención para determinar los efectos de dirección de la asimetría de la profundidad radicular en los resultados del ensamblaje.

Como apuntan nuestros resultados, la variabilidad climática anual tiene una especial relevancia en el establecimiento y desarrollo de nuestras comunidades (Capítulos 1 y 2). Nuestros resultados parecen indicar, como ya se había estudiado previamente (Sánchez et al., 2022; Peralta et al., 2019) que solamente bajo un potente estrés hídrico, observaremos una marcada selección de rasgos. Como durante el desarrollo del experimento solo hemos experimentado un año con precipitaciones inferiores a la media (2019) no hemos podido comprobarlo. Por lo que, necesitaríamos extender nuestro estudio para tener esos datos. Además, según diferentes estudios, el cambio climático afectará especialmente a las regiones áridas y semiáridas como la aquí estudiada (IPCC, 2022). Por lo tanto, entender cómo esta variabilidad climática, y concretamente, la disponibilidad hídrica, afecta a nuestras comunidades es de especial importancia y relevancia tanto para tratar de mitigar los efectos adversos ofreciendo herramientas y diferentes soluciones de gestión, tanto preventivas como encaminadas a la restauración ambiental.

Siguiendo con la idea de aportar información para la gestión y restauración ambiental, cabría señalar que las zonas con presencia de CBS presentaron unas composiciones de especies muy similares a las zonas inicialmente de suelo desnudo al cuarto año. Esto podría explicarse por el hecho de que, a partir del cuarto año, la CBS se estableció en estas zonas. Este resultado contrastaría con estudios anteriores (Kidron et al., 2020) que describían la recuperación de la CBS como un proceso mucho más lento que el que hemos presenciado nosotros en el campo. Aunque la CBS que comenzó a establecerse en el suelo desnudo probablemente no sea tan diversa como una CBS bien conservada y desarrollada, ejerció un papel similar para el establecimiento de especies anuales.

En este estudio nos hemos centrado en estudiar la comunidad en su conjunto, solamente en el Capítulo 3 hemos abordado el efecto en las especies de manera individual. Como observamos en ese capítulo (Ortiz et al., 2023), los individuos de una misma especie variaban su altura dependiendo de las condiciones. La variabilidad intraespecífica de las especies anuales es otro aspecto que explorar, ¿podría la plasticidad fenotípica ayudarnos a entender el rango de condiciones de estrés ambiental que una planta anual puede llegar a soportar? Del mismo modo, se plantea la duda de como ciertas especies que se conocen como especies clave modulan los efectos de los factores abióticos y bióticos y como afectan a la coexistencia de las plantas. ¿Podría alguna planta anual actuar como planta facilitadora? como se ha visto con *Carthamus tenuis* (Boiss. & Blanche) Bornm (Madrigal-González et al., 2020). Por lo tanto, más estudios manipulando la identidad de las especies y controlando tanto la diversidad funcional como filogenética de la comunidad nos ayudará a resolver algunas de estas preguntas relacionadas con la interacción planta-planta dentro de la comunidad que se han quedado sin respuesta.

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GENERAL CONCLUSIONS

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The current research allows us to draw the following conclusions:

1. The structure of the annual-dominated plant communities in dryland gypsum systems is determined by both stochastic (such as the arrival of propagules) and deterministic processes (presence of *M. tenacissima* plants and biological soil crust -BSC-); the contribution of each modulator type to the assembly of the community is driven by the high rainfall variability typical of our study site.
2. The dominant biotic components in the Iberian gypsum systems (*M. tenacissima* perennial grass tussocks and the biological soil crusts) favour the creation of microenvironments that influence community formation. These biotic factors influence richness, total plant cover and taxonomic diversity. However, it seems that when abiotic conditions (water availability) are favourable, they do not generate a clear selection of species based on their functional traits. Furthermore, this would confirm the importance of water availability as a key factor in the assembly of our community.
3. From the analysis of assemblage features during four consecutive years, we can infer that seed banks in dryland gypsum systems take longer to recover than previously thought. Despite the active primary and secondary dispersal in gypsum steppes, mainly the presence of BSC may accelerate the seed bank recovery process, by promoting seed trapping and retention. This finding emphasizes the importance of preserving intact, well-structured BSC.
4. Biological soil crusts, dominated by lichens in dryland gypsum systems, represent a high source of heterogeneity, affecting in a complex and multifaceted manner the gypsophilous annual plant life cycle. Firstly, acting as a powerful seed-trapping agent and then imposing a physical barrier to the establishment of plants, especially by intact portions of BSC and for species with large seeds. However, plants that successfully establish will benefit from the amelioration of microenvironmental conditions by the presence of BSC, increasing plant growth and fitness.
5. Presence of *Macrochloa tenacissima* tussocks in the Iberian gypsum systems did not play a clear facilitating role during the process of community assembly. While

shallow tussock roots of this perennial grass species seem to intensely compete with seedlings establishing in the vicinity, the aerial part may do not exert any clear nurse effect on neighbour assemblages.

6. Annual plant communities in dryland gypsum systems may be strongly organised around competitive relationships, which would make niche complementarity one of the central mechanisms of assembly under water stress conditions, allowing the coexistence of multiple species and also explain the high diversity typically characterising assemblages.
7. Our results demonstrate the importance of plant neighbourhood in determining the ability of annual plants to complete their life cycles and their reproductive success within assemblages. Although gypsophilous species are adapted to the climatic variability characterising semi-arid gypsum systems, they show differences in performance depending on the functional and/or phylogenetic properties of the community, both with and without water restrictions.
8. The initial functional diversity of assemblages as a result of their species composition notably drives the assemblage mechanisms of gypsophilous communities. In scenarios with high functional diversity (related to plant stature —i.e., maximum plant height— in our study) niche complementarity predominated, enhancing plant fitness, whereas in those with low functional diversity (i.e., scenarios with only small or large plants) species invested more resources in growing and competing in height than in reproduction.
9. We confirm that the initial phylogenetic diversity of gypsophilous annual plant assemblages could be a good indicator of plant survival and reproductive success. Plants growing in higher phylogenetic diversity scenarios fructified earlier and thus completed their life cycle shorter than those in scenarios formed by close phylogenetically related species. Furthermore, under drought conditions, more plants were able to fructify in high phylogenetic diversity scenarios and furthermore, they produced more seeds per fruit than in low phylogenetically diverse scenarios. Therefore, phylogenetically more diverse communities seem to be more resilient to water stressful events. It seems that, in gypsophilous annual plant communities, phylogeny may work as a good proxy of species niche, summarizing the overall ecological balance of traits of different nature (i.e.,

morphological, physiological, metabolic, phenological) most of which might be hard or impossible to measure.

10. Functional and phylogenetic diversity provide complementary information to explain assembly and coexistence processes. While phylogenetic diversity is an excellent predictor of complementarity mechanisms, functional diversity, in the form of a multi-trait index, allowed us to explain part of the variability in reproductive success in gypsophilous annual plant community. Probably because phylogenetic diversity integrates the entire evolutionary history of species and functional diversity more recent evolutionary changes.