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Facilitation enhances ecosystem function with non-random species gains

Jose A. Navarro-Cano, Marta Goberna and Miguel Verdú

J. A. Navarro-Cano (https://orcid.org/0000-0001-8091-1063) and M. Goberna (https://orcid.org/0000-0001-5303-3429), Depto de Medio Ambiente y Agronomía, Centro Nacional Inst. de Investigación y Tecnología Agraria y Alimentaria, INIA-CSIC, Madrid, Spain. – M. Verdú (https://orcid.org/0000-0002-9778-7692) ✉ (miguel.verdu@ext.uv.es), Depto de Ecología Vegetal, Centro de Investigaciones sobre Desertificación (CSIC-UVEG-GV), Moncada, Valencia, Spain.

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Facilitation, an ecological interaction assembling plant communities worldwide, has been shown to modulate both species richness and ecosystem functions. Such a biodiversity–ecosystem functioning (BEF) relationship can be decomposed into different components not only related to species losses and gains but also to the identity of the species and the context in which they live. Using an extension of the classical BEF approach named CAFE (community assembly and the functioning of ecosystems), we quantified the contribution of these components to the BEF relationship in a Spanish semiarid plant community shaped by facilitation. We used species richness as a measure for biodiversity and plant cover as a proxy of multiple ecosystem functions including plant productivity, soil protection, soil fertility and microbial productivity. Nurse plants doubled the number of species that live beneath them relative to open ground, but caused a five-fold increase in plant cover. The disproportionate increase of plant cover was a consequence of the identity of the species enhanced by nurse plants, which were more productive than the average. We discuss these results in terms of sampling effects (i.e. the higher probability of richer communities to harbour hyperproductive species) and complementary effects (i.e. richer communities enhancing productivity through resource partitioning, abiotic facilitation or biotic feedbacks). The enhancement of ecosystem functions that plant facilitation produces by incorporating species with high functional values to the community may reverberate among other trophic levels and propagate beyond the local scale where the ecological interaction is produced.

Keywords: community assembly, ecosystem function, plant facilitation

Introduction

The existence of a relationship between biodiversity and ecosystem functioning (BEF) was the center of a profound ecological debate that spurred hundreds of empirical studies (Tilman et al. 2014). At present, there is ample evidence that biodiversity is positively related to ecosystem function (Cardinale et al. 2002, Balvanera et al. 2006, Wagg et al. 2014). A potential, and overlooked, mechanism driving positive BEF relationships is interspecific facilitation (Wright et al. 2017, Barry et al. 2019). Indeed, facilitation has

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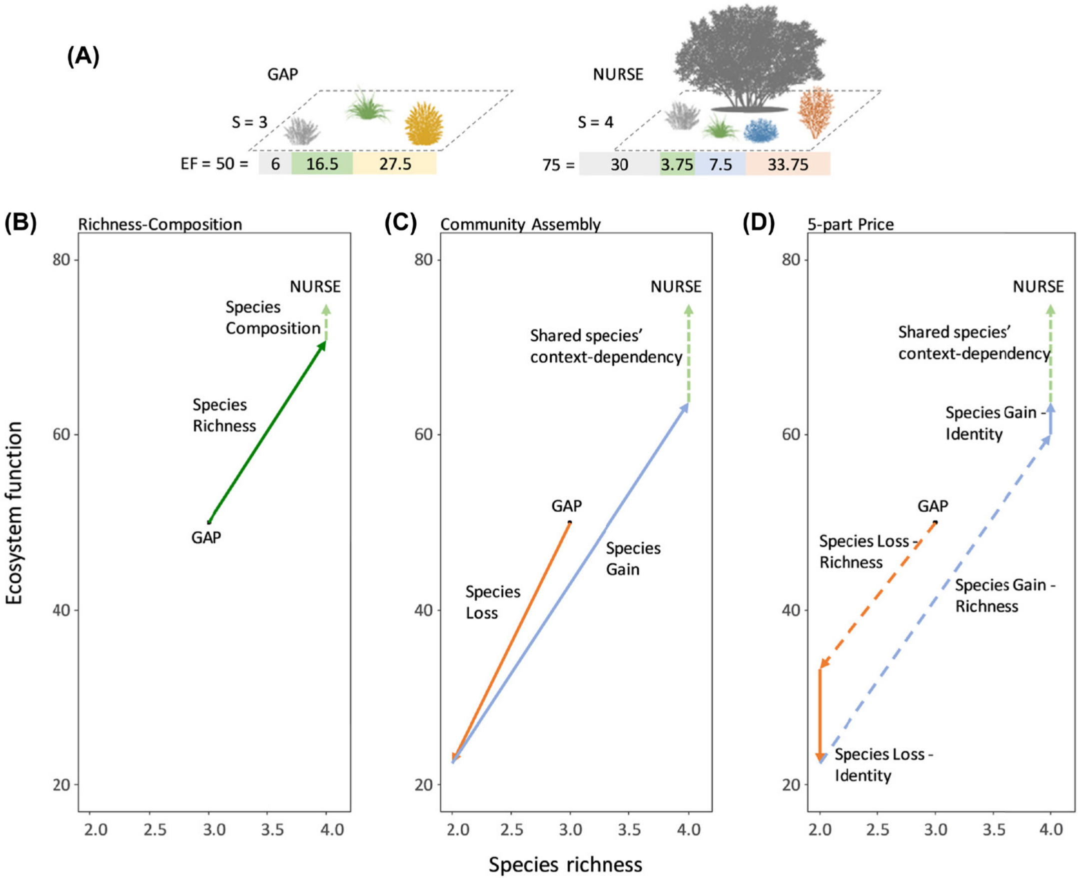
been shown to increase both diversity (Soliveres et al. 2011, Cavieres et al. 2014) and ecosystem functions (Mulder et al. 2001, Ellison et al. 2005). Currently, experimental studies are also including facilitation as a mechanism underlying positive BEF relationships (Wright et al. 2021).

Plant facilitation is an ecological interaction through which a (nurse) plant promotes the establishment of other (facilitated) species that take advantage of the modified environmental conditions under the nurse canopy (Callaway 2007). These new, usually more humid, shaded and fertile conditions, promote the establishment of stress-sensitive species under nurse canopies but, at the same time, may preclude the establishment of stress-tolerant species (Valiente-Banuet et al. 2006). In addition, facilitation interactions may reverse to competition with time (Miriti 2006). Thus, the balance between facilitation and competition may concomitantly produce species losses and gains. In general, species with traits that are different from those of nurse plants tend to be enhanced via facilitation but later competition among facilitated species drives species loss (Valiente-Banuet and Verdú 2008). This is the reason why the outcome of the interactions between facilitated species are context-dependent and determined by the species composition of the neighbourhood (Castillo et al. 2010, Schöb et al. 2013).

Both gains and losses of species have profound and interdependent impacts on ecosystem function and therefore an explicit integration of both processes is required to relate biodiversity with the functioning of ecosystems (Wardle et al. 2011). Facilitation, by modulating species losses and gains, has important consequences on the provision of ecosystem functions (Badano and Marquet 2009, Navarro-Cano et al. 2014). Wright et al. (2017) delimitate abiotic and biotic mechanisms through which facilitation may drive BEF relationships. The abiotic mechanisms are related to the amelioration of microclimatic conditions and to the nutrient enrichment of the microhabitat in the presence of numerous species. The biotic mechanisms are produced via diversity effects, with species growing in diverse neighbourhoods being more productive by providing complementary functions, sharing defences against pathogens and/or attracting mutualists. Indeed, species-rich neighbourhoods under nurse plants may enhance plant productivity by alleviating the stress conditions, enriching the resources of the microhabitat, dissuading antagonists (i.e. pathogens), attracting mutualists (i.e. mycorrhizal fungi and rhizobacteria) and provisioning complementary functions by reducing the competitiveness of dominant plants through indirect interactions (Soliveres et al. 2011, Filazzola and Lortie 2014, Aschehoug and Callaway 2015, Rodríguez-Echeverría et al. 2016).

Since the seminal study of Connell and Slatyer (1977), facilitation has been recognized as a process driving community assembly. Therefore, species losses and gains occurring in facilitation-shaped ecosystems are not randomly produced, but follow community assembly dynamics. For example, germination experiments under controlled conditions showed that species requiring facilitation tend to have larger biomass than those species not requiring nurse plants (Butterfield and Briggs 2011), suggesting that facilitation favours productive species. Bannar-Martin et al. (2018) advocated the integration of community assembly mechanisms to properly understand the BEF relationship. Taking into account community assembly is especially important as non-random biodiversity changes occurring in real-world may be altering ecosystem functions more than controlled experiments are showing (Zavaleta and Hulvey 2004, Bracken et al. 2008). Based on Fox and Kerr (2012)'s ecological application of the Price equation, Bannar-Martin et al. (2018) have developed an approach that allows us to study how changes in species richness and community assembly simultaneously impact ecosystem function. The Price equation approach separates the effect of species richness from that of species composition by running pairwise comparisons between sites. Teasing apart richness and composition is crucial when poor-species sites are not subsets of richer sites and therefore, the identity of different species between sites might be ultimately driving the ecosystem function (Fox and Kerr 2012). The ecological-extended Price equation method, named CAFE (community assembly and the functioning of ecosystems) expands the simple BEF approach (Box 1B) by decomposing the relationship between plant facilitation and ecosystem function through different components, such as species losses and gains (Box 1C) as well as identity and context-dependency effects (Box 1D). Unlike other methods aimed to unravel the shape of the relationship between mean ecosystem function and species richness, CAFE is developed to compare the biodiversity effects on ecosystem functions between paired sites. CAFE has been shown to capture the performance of individual species at paired sites and to correctly describe complex, non-linear, non-additive mechanisms affecting species richness, composition and species' functional contributions (Fox and Kerr 2012). We apply this method to unravel the BEF relationship in a community shaped by plant facilitation in a semiarid area from southeastern Spain where previous studies have shown that plant communities under nurse plants are more diverse and provide higher rates of ecosystem functions than those on the open ground (Navarro-Cano et al. 2014, 2015, 2016a, Goberna et al. 2016). We selected species richness as a measure of biodiversity and plant cover as a proxy of multiple ecosystem functions. Plant cover is related to plant productivity and soil protection in general (Durán-Zuazo and Rodríguez-Pleguezuelo 2008) and, in our study site, it also promotes functions related to soil fertility and microbial productivity (Navarro-Cano et al. 2015). Plant cover is also an easy-to-interpret variable that helps illustrate the complex BEF relationships and the usefulness of the CAFE approach. We hypothesize that the enhancement that nurse plants simultaneously produce in species richness and plant cover is the result of 1) the species gained under nurse plants being more productive (Butterfield and Briggs 2011) and 2) diverse neighbourhoods promoting productivity (Wright et al. 2017).



Box 1. Three different arrangements of the overall species effects on a hypothetical ecosystem function. (A) Schematic representation of the CAFE relationship mediated by facilitation where a plant community living on a gap (left) is compared to another community under a nurse canopy (right). The plant community living in the 'gap' is composed by three species ($S = 3$) that provide, in total, 50 units of ecosystem function ($EF = 50$) while the community under the 'nurse' amounts 75 EF units with four species. Each species contributes with a different magnitude to the ecosystem function (e.g. the grey species contributes 6 EF units in the gap and 30 under the nurse). In this example, the most diverse community has also the highest EF magnitude, indicating a positive BEF relationship. The assembly of plant communities under nurse plants entails species losses (yellow species) and gains (blue and brown species). However, not all the species are functionally similar: while some species provide EF values higher than the average per-species function of the community (e.g. yellow species in the gap and grey and brown species under the nurse), others provide lower values (e.g. grey species in the gap and green and blue species under the nurse). Context-dependency effects also occur when the same species behave differently in the two communities (e.g. grey species increases its EF under nurses from 6 to 30, while green species decreases it from 16.5 to 3.75). (B–D) The statistical CAFE approach places the plant community under the nurse cover and its paired gap community in a bidimensional space defined by species richness in the x-axis and ecosystem function in the y-axis. Then, the net difference between both communities is decomposed into species losses, species gains, species composition and context-dependency effects. (B) reflects a simple BEF relationship and decomposes the trajectory between both communities in two vectors depicting 1) the species richness effect and 2) the species composition effect. In this case, the net gain of one species in the plant community under canopy yields an increase in EF from 50 to 71 ('species richness'). Beyond species richness, the combined composition effects under nurses (i.e. gains of productive species, losses of unproductive species and changes in resident species' functions) results in an extra EF increment from 71 to 75 ('species composition'). (C) accounts for the community assembly process by using three vectors capturing 1) species losses, 2) species gains and 3) context-dependent effect of the shared species. In this case, the loss of one species reduces EF from 50 to 22.5 ('species loss') but the gain of two species increases EF from 22.5 to 64 ('species gain'). Furthermore, the shared species are, on average, more productive under the nurse canopy and increase the final EF from 64 to 75 ('shared species context-dependency'). (D) decomposes the trajectory into 5-part Price vectors: 1) species richness effect of losses, 2) species identity effect of losses, 3) species richness effect of gains, 4) species identity effect of gains and 5) context-dependent effect of the shared species. Losing one species randomly from gaps decreases EF ('species loss – richness'). As the species lost from gaps had a higher function than average per-species function of the gap, their loss yields an extra EF reduction ('species loss – identity'). Gaining two species randomly from gaps greatly increases EF ('species gain – richness'). However, the average function of the gained species is not very high and therefore the extra increment of the EF in the community is moderate ('species gain – identity'). Finally, the shared species in both communities are, on average, more productive under the nurse canopy, increasing the EF ('shared species context-dependency').

Methods

Study site

The study was run in gypsum outcrops from southeastern Spain (Crevillent, Alacant; 30º16'19''N, 0º50'19''W; average 350 m a.s.l.) under a semiarid Mediterranean climate (240 mm mean annual rainfall, 20°C mean annual temperature). Vegetation is mainly shaped by the abundant gypsophyte shrub *Ononis tridentata* that facilitates the establishment of many other species in the community, producing a patch-gap mosaic with an overall 25% plant cover (Navarro-Cano et al. 2014, 2015, 2016a for a description of the study site and the role of *O. tridentata* individuals as nurse plants assembling the community through plant facilitation).

Sampling procedure and statistical analysis

We selected 25 plots under the nurse plant *O. tridentata* canopy and 25 adjacent gaps of the same size to estimate the cover of each plant. Most of the species richness in each microhabitat was captured with 25 plots, as the flatten species accumulation curves reveal (Supporting information). The size of the plots varied with the size of the nurse plant, ranging from 11 435 to 21 980 cm^2. The cover of facilitated plants was estimated by adding the number of cm that each plant species occupied along a variable number of parallel linear transects established under the canopy of the nurse plant. The number of transects ranged between 7 for the smallest nurse plants and 19 for the largest nurse plants. The length of the transects were proportional to nurse plant size and ranged between 720 and 2738 cm. The total length sampled below nurse plants averaged 1452 ± 502 cm. For each nurse plant plot, we established an adjacent plot (1.5 m apart) on the open ground (i.e. gap). This plot had the same area and was sampled with identical number and length of transects as the nurse plant plot.

To estimate the contribution of different processes to the BEF relationship, we followed the CAFE approach described in Bannar-Martin et al. (2018) and portrayed in Box 1. We first assessed whether poor-species plots were subsets of paired rich-species plots by estimating the relative contribution of species turnover and nestedness to the total beta-diversity. To do so, we used the betapart command with the Jaccard dissimilarity index in the betapart R package (Baselga et al. 2018). We then calculated the length of all the CAFE vectors related to species losses, gains, compositional, identity and context-dependent effects in the priceTools package for R (Kremer 2020). The vectors were obtained for each of the 25 plot pairs, and we assessed whether their mean lengths differed from zero through non-parametric exact Wilcoxon tests. We run the analyses both including and excluding the nurse plant to allow comparisons with other studies that estimate the performance of both facilitated and nurse plant species (Wright et al. 2017).

Results

A large portion of the beta-diversity between nurse and gap paired plots ($\beta = 0.83$) was due to species turnover (80%) while nestedness represented only 20%. This result reveals the need of teasing apart the effects of richness from those of species composition in ecosystem functions.

We identified 42 species facilitated by *Ononis tridentata* with a mean cover ranging from 0.002 to 6.45% (Supporting information). *Brachypodium retusum*, *Sedum sediforme* and *Fagonia cretica* contributed an average of 56% of the total cover of nurse plots. The species contribution to plant cover in gaps was more diffuse, with *Teucrium libanitis*, *Diplotaxis harra* and *Globularia alypum* as major contributors to plant cover providing just 11% of total cover per gap.

Plant communities under nurse canopies were more diverse (8.8 ± 0.6 species; mean ± SE) than in the gaps (4.3 ± 0.4) ($V = 6$; $p < 0.001$; two-sample paired Wilcoxon test). This approximately two-fold increase in species richness yielded more than a 5-fold increase in plant cover (from 6.3 ± 0.8% to 34.1 ± 4.5%; $V = 1$; $p < 0.001$; two-sample paired Wilcoxon test). This disproportionate increase was decomposed into a large species richness effect (82%; species richness vector in Fig. 1 left) and a smaller, but significant, species composition effect (18%; species composition vector; $V = 239$; $p < 0.001$; one-sample Wilcoxon test; see individual values in the Supporting information) indicating that plant cover increased under the nurse canopy not only as a function of richness but also as a result of changes in community composition, as explained below.

The positive species richness effect was due not only to the larger number of gained versus lost species but also to the differential contribution of these species to the overall cover. The loss of 2.4 species represented a 4.1% reduction in plant cover (species loss vector in Fig. 1 center, Supporting information) while the gain of 6.8 species represented an increase of 30.3% in plant cover (species gain vector). Thus, the plant cover added per each gained species was 2.6 times greater than the cover lost per each lost species. The context-dependent effect of the shared species (Shared species' context-dependency vector) although positive, was not significantly different from zero ($V = 164$; $p = 0.10$; Supporting information), indicating that, on average, the species that occurred both in gaps and under nurse plants showed a similar cover regardless of the microhabitat.

Species identity effect of losses was very small but significantly different from 0 (species loss – identity vector $= -0.48$; $V = 51$; $p = 0.02$; Fig. 1 right) indicating that species lost from gaps provided slightly more cover than the average species in the gap community. Finally, species identity effect of gains was significantly higher than zero (species gain – identity vector $= 3.85$; $V = 206$; $p = 0.008$; Supporting information) suggesting that species that were added in nurse plots provided a greater contribution to plant cover than average species of the nurse plot community.

The nurse plants, *O. tridentata*, provided 30–93% of plant cover in their plots. When this species was included in the

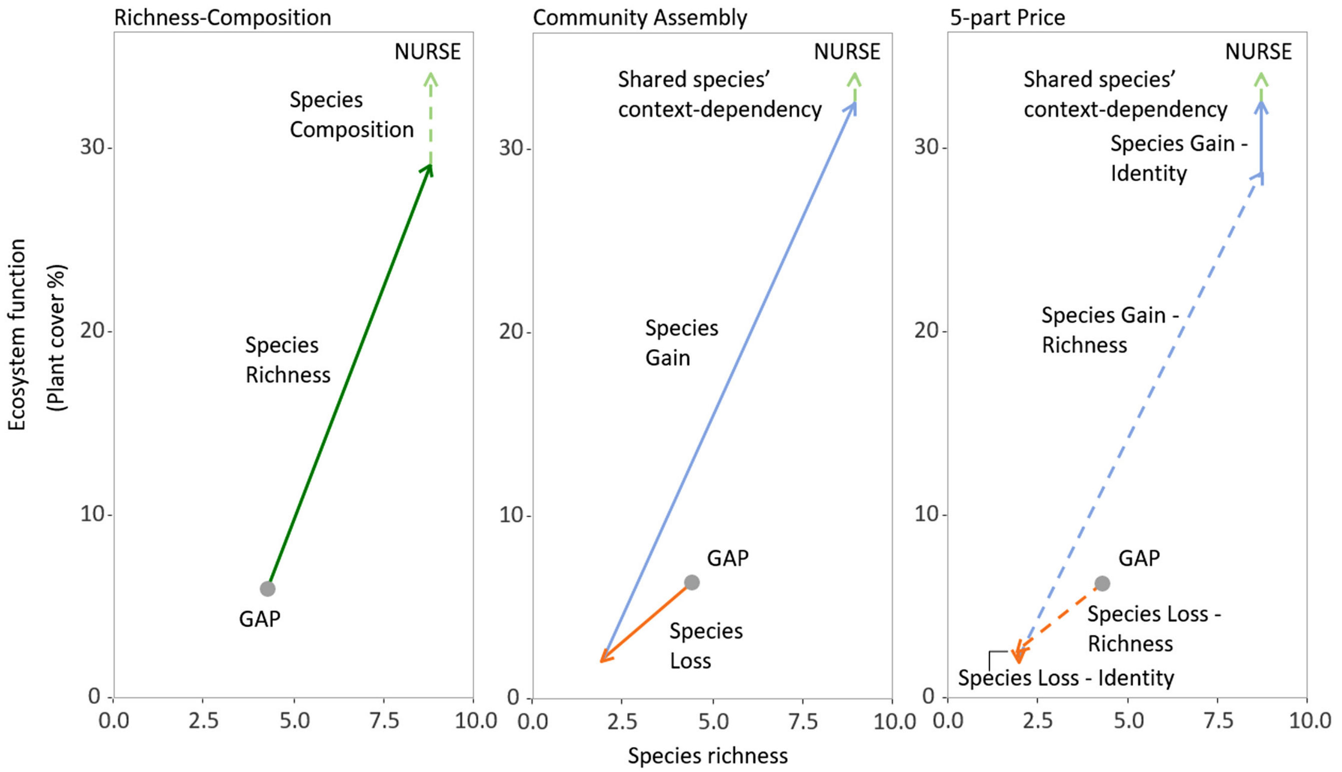


Figure 1. Decomposition of biodiversity–ecosystem function (BEF) relationship in the plant communities living in the gap and under *Ononis tridentata* nurses. Plant cover was used as a proxy for multiple ecosystem functions and species richness as a measure of biodiversity. See Box 1 for the meaning of each vector depicting the BEF trajectory. Each vector is the average of 25 nurse-gap paired plots. See the Supporting information for the individual values of the 25 vectors as well as the means and standard deviations.

CAFE analyses, the conclusions were strongly similar to those obtained without *Ononis*. Obviously, the average plant cover in nurse plots was larger but the statistical significances of the vectors did not change (see the Supporting information to compare the results with and without *Ononis*).

Discussion

Facilitation by nurse plants concomitantly increased species richness and plant cover, a proxy for multiple ecosystem functions in our study system (Navarro-Cano et al. 2015). These results underscore the importance of plant facilitation as a mechanism enhancing biodiversity and ecosystem functioning (Wright et al. 2017, 2021).

Nurse plants caused a five-fold increase in plant cover just doubling the species richness under their canopy. This means that the increase of EF in plant communities under nurse plants was not only due to a species richness effect but also to a species composition effect. Indeed, a large proportion of the beta-diversity between nurse and gap paired plots was due to species turnover, indicating the taxonomic compositional differences between both microhabitats. While the species inhabiting gap plots tend to have traits associated with tolerance to gypsum soil toxicity and to acquisition of water from deeper soil layers, species requiring nurse plants to recruit lack these stress-tolerance mechanisms (Navarro-Cano et al. 2016a, Sánchez-Martín et al. 2021). The differential composition of species under nurse plants was translated into disproportionately higher covers because gained species were more productive than the average. This increase in productivity can be mediated both by sampling and complementarity effects (Wright et al. 2017, Michalet et al. 2021).

Sampling effects refer to the higher probability of diverse neighbourhoods to contain hyperproductive species. Indeed, our data show that the probability to find hyperproductive species (*Brachypodium retusum*, *Sedum sediforme* and *Fagonia cretica*) increased with species richness (Spearman correlation $r=0.51$, $r=0.51$ and $r=0.70$ respectively; all p-values < 0.001). Given that these three species, especially the rhizomatous perennial grass *B. retusum*, are able to provide around half of the overall plant cover, facilitation-mediated BEF relationship could be driven by sampling effects.

Complementarity effects could be at work if growing in diverse neighbourhoods enhances productivity through resource partitioning, abiotic facilitation or biotic feedbacks (Barry et al. 2019). Previous work supports all these three components. Resource partitioning is strongly suggested by the high functional and phylogenetic diversity of plant communities under nurse plants (Castillo et al. 2010). Indeed, nurse plants in gypsum soils promote the coexistence of phylogenetically-distant facilitated species that explore different niches thanks to trait differences in plant height, root depth/spread quotient, root intensivity, gypsophily and xerophily (Navarro-Cano et al. 2016b). Abiotic facilitation is largely known from multiple studies showing how plants ameliorate the microhabitat for their neighbours providing resources or alleviating the physical stress (Callaway 2007). Biotic feedbacks between soil microbes and plants are also known to be enhancing plant productivity in communities under nurse plants (Rodríguez-Echeverría et al. 2016). Although previous works confirm that the three mechanisms are operating in our study system (Navarro-Cano et al. 2015, 2016a, b, Goberna and Verdú 2018), it is difficult to quantify the relative contribution of each of them to complementarity. However, we can explore whether an average context-dependency effect exists; that is, whether the same species performs better under nurse canopy than in the gap. For example, shade-tolerant species may perform better under nurse plants than on the open ground (Kothari et al. 2021). In our case, context-dependency effects were not significantly different from zero. However, this statistical result should not be interpreted as a general failure of species to grow more under nurses, but rather as the average growth response of some species being benefitted and some others being hindered by nurse canopies. For example, species like *Anthyllis cytisoides* and *Fumana thymifolia* provided more cover to gaps than to nurse plots, while the opposite was true for *Brachypodium retusum* and *Rhamnus lycioides* (Supporting information).

Altogether, these results suggest that species are not interchangeable in terms of the functions they provide to the ecosystem. In our case, the identity of the species gained through facilitation is relevant for explaining the higher plant cover under nurse plants. In short, facilitation can increase ecosystem functions via non-random species gains, that is, incorporating species with high functional values. Facilitation occurs at fine spatial scales but can have important consequences on the provision of ecosystem functions (Badano and Marquet 2009, Navarro-Cano et al. 2014) that might ultimately propagate to other trophic levels and reverberate in adjacent ecosystems (Losapio et al. 2019, 2021, Collins and Baxter 2020).

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Author contributions

Jose A. Navarro-Cano: Data curation (lead); Formal analysis (equal); Investigation (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Marta Goberna**: Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (lead); Supervision (equal); Validation (equal); Visualization (lead); Writing – review and editing (equal). **Miguel Verdú**: Conceptualization (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (equal); Methodology (lead); Project administration (lead); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.9zw3r22g0> (Navarro-Cano et al. 2021).

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