

The facilitative effects by seeds and seedlings on emergence from the seed bank of a desert annual plant community¹

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Abstract: Facilitation is important in structuring plant communities in harsh environments although most recent studies have been descriptive and focussed on adult plant interactions. Here, we test for facilitative effects by seeds and seedlings of *Erodium laciniatum* and *Erucaria pinnata* on the emergence and subsequent community structure from an annual plant seed bank in the Negev desert, Israel. We specifically test whether (i) the addition of seeds or seedlings of these species increases emergence from the seed bank, (ii) the addition of seeds or seedlings increases final plant community performance, and (iii) the effect of each species is specific. Both *Erodium* seeds and seedlings acted as a benefactor for the rest of the plant community by increasing density and biomass of the plants germinated from the seed bank. *Erodium* seedlings had a stronger positive effect than seeds early in the growing season. *Erucaria* (seeds and seedlings) did not influence the plant community. This suggests that species interactions are specific and that interactions between seeds and between plants and seeds can influence community structure.

Keywords: facilitation, nurse-plant, focal species, annuals, stress, *Erodium laciniatum*, *Erucaria pinnata*.

Résumé : La facilitation joue un rôle important dans la constitution des communautés végétales dans les environnements hostiles. Toutefois, la plupart des études récentes sur le sujet ont été descriptives et se sont concentrées sur les interactions entre les plantes du stade adulte. Dans cette étude, nous vérifions si les graines et les plantules d'*Erodium laciniatum* et d'*Erucaria pinnata* facilitent l'émergence et sont responsables de la structure d'une communauté végétale du désert de Negev, en Israël. De façon plus précise, nous avons vérifié (i) si l'ajout de graines ou de plantules de ces espèces favorise l'émergence des graines qui se trouvent dans le sol, (ii) si l'ajout de graines ou de plantules accroît la performance finale de la communauté végétale et (iii) si l'effet de chaque espèce est spécifique. Les graines et les plantules d'*Erodium* ont un effet bénéfique sur la communauté végétale dans son ensemble car elles augmentent la densité et la biomasse des plantes issues du réservoir de graines. Les plantules d'*Erodium* ont plus d'impact que les graines au début de la saison de croissance. Les graines et les plantules d'*Erucaria* n'influencent pas la communauté végétale. Il semble donc que les interactions entre les espèces soient spécifiques et que les interactions entre les graines ainsi qu'entre les plantes et les graines puissent influencer la structure de la communauté.

Mots-clés : facilitation, plante abri, espèces cibles, plantes annuelles, stress, *Erodium laciniatum*, *Erucaria pinnata*.

Introduction

Most research on facilitation, outside the context of succession, has focussed on interactions among adult plants (Callaway, 1995). This bias restricts the understanding of facilitation among species and does not provide insight into size-related effects, temporal effects, or interactions between other life-history stages such as seeds and seedlings. An additional bias occurs if measurements are recorded only at the end of an experiment because these fail to distinguish between the outcome of facilitation and the process by which this outcome was produced; this distinction has also been noted in competition studies (Gibson *et al.*, 1999). In this paper, we address both of these aspects and explicitly test for facilitative effects by seeds and seedlings on emergence from the seed bank of an annual plant community, including subsequent effects measured throughout the growing season. This allows us to test for more subtle interactions among congeneric (similar-sized)

annual plant species at the seed and seedling level rather than at the shrub-understorey level that is common in the facilitation literature (Callaway, 1995).

There are two general categories of studies that have tested small-scale seed-related effects. The first category, studies of the effect of different seed densities, has generally detected density-dependent emergence (Palmblad, 1968; Linhart, 1976; Waite & Hutchings, 1978, 1979; Adler *et al.*, 1993; Murray, 1998) and accelerated emergence times (Ross & Harper, 1972; Inouye, 1980; Miller, 1987; Bergelson & Perry, 1989; Dyer, Fenech & Rice, 2000). The second category of experiment has focussed either on the effect of previously planted seeds on the germination of other seeds (Black & Wilkinson, 1963; Bergelson & Perry, 1989) or on the effect of existing adult vegetation on the germination of planted seeds (Ross & Harper, 1972; Shaw & Antonovics, 1986; Fowler, 1988; Bergelson, 1990; Ryser, 1993). While this category of experiment is unique in that specific effects of particular seeds or plants are tested (seed-seed and plant-seed interactions), unfortunately, only two-species mixtures have been used and only germination, and not subsequent emergence, have been tested.

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In this study, we investigate the following hypotheses to test for specific effects, both early and mid-season, of two of the largest annual species in our system (hereafter called focal species) on emergence from the seed bank of a desert annual community. (i) The addition of seeds or seedlings of the focal species will increase emergence of seeds from the seed bank. (ii) The addition of seeds or seedlings of the focal species will increase some final plant community measures such as total adult plant density, final biomass, or final biomass/plant. (iii) The effects of each focal species on the seeds and emergent vegetation are species specific.

Methods

SEED COLLECTION

Seed was collected in November 1998 and November 1999 at Bir Asluj in the Holot Mashabim Nature Reserve (31°00.212' N, 34°44.474 E, mean annual precipitation 110 mm) in the central Negev desert, Israel. The herbaceous vegetation is entirely annual and seed bank based. There are typically about 20 species in this community (area of dune about 1 ha) (Dyer *et al.*, 2001). We collected the top 2 cm of sand, which effectively samples at least 99% of the total seed bank (Venable, 1989). Virtually all the seed was separated from the sand with 500- μ m sieves, and the natural seed bank density (hereafter called 1 \times) for the field site was calculated to be 600.8 g m⁻² (Goldberg *et al.*, 2001). The experiments were done in pots in an open air greenhouse at the Mitrani Department for Desert Ecology Research, 25 km southeast of the site where the seed was collected.

EXPERIMENT 1 (1999): ADDITION OF SEEDS OF THE FOCAL SPECIES TO THE SEED BANK

We tested the effect of adding seeds of the two focal species, *Erodium laciniatum* (Cav.) Willd. and *Erucaria pinnata* (Viv.) Taekh. et Boulos, to the 1 \times density seed bank (with no other seeds of these focal species present). We sowed seed in the following ways: 1 \times seed bank spread evenly + a group of 5 seeds of *Erodium* or *Erucaria* placed in the middle of each pot; 1 \times seed bank + 10 seeds of *Erodium* and *Erucaria* (5 seeds of each); and seed bank only (no additional focal seed). We also sowed 5 seeds of each of the focal species by themselves without seed bank, allowing us to test for a reciprocal effect of the seed bank on the focal species. We repeated all plantings 10 times at two irrigation levels, using a randomized block design. The low water treatment was equivalent to the long term annual average of 110 mm, and the high water was equivalent to 150 mm per annum, levels similar to that applied by Goldberg *et al.* (2001) using seed from the same study site.

Seed was sown on January 15, 1999 in 15-cm diameter pots filled with seedless sand from the dune where the seeds were collected. The planting density of seed was equivalent to the natural seed density in the field, *i.e.*, 6 g of seed per 10 \times 10 cm. A buffer strip of 4.5 cm was left in each pot to minimize edge effects. The pots were surveyed once a week for the first three weeks and every two weeks thereafter to the end of the natural growing season in mid-April.

To control for the effects of disturbance caused by emergence of the larger focal species, *i.e.*, cotyledonous

leaves disturbing the sand, an artificial mimic of the disturbance was also applied to the seed bank planted without any of the seeds of the focal species specifically added. In these pots, after the seed bank was in place, a 15 \times 3 cm wooden tongue depressor was used to gently stir up the middle of the pot. The depressor was then "planted" and left in the middle of the pot for the remainder of the experiment.

ANALYSES FOR EXPERIMENT 1

The effect of adding seeds of the focal species (and mimic) on emergence and subsequent plant density, biomass, and number of species was analyzed with repeated-measures ANCOVA with census and water level as main effects (and interaction effects) and the mass of the additional 5 or 10 seeds as the covariate. To test for the effect of the seed bank on the emergence of the focal species, we compared the mean emergence of *Erodium* or *Erucaria* with seed bank, of both sown together with seed bank, and of each sown independently, with ANOVAs at both water levels and interaction effects. Specific differences between groups were tested with post-hoc contrast analyses at $p < 0.05$.

EXPERIMENT 2 (2000): ADDITION OF SEEDLINGS OF THE FOCAL SPECIES TO THE SEED BANK

We tested the effect of adding seedlings of three focal species to ungerminated and germinated seed bank at two different times, the beginning of the natural growing season and 6 weeks later in mid growing season. We planted the seed bank at natural seed density (1 \times) in 15-cm pots and followed the same procedures as in the first experiment. Controls received only seed bank while treated pots received seed bank and a seedling of the focal species planted in the middle of the pot. These seedlings were germinated individually in pots two weeks in advance. Three species of seedlings were independently added on January 15, 2000 to the pots with seed bank: *Erodium laciniatum*, *Erucaria pinnata*, and *Trifolium tomentosum* L.. The first two are large annuals in the field and the last is a smaller annual.

To add the seedlings of the focal species to the neighbourhoods (in both early and mid-season), we used a small metal spatula to place the seedling and a core of seedless sand with intact roots into the pots with seed bank. For the mid-season seedling additions, we placed the seedlings and core as close as possible to the middle of the pots without disturbing the vegetation growing in that region. In both cases, we recorded the density of the neighbourhood in the pot once a week for the first two weeks and every two weeks thereafter for the remainder of the growing season to mid-April.

ANALYSES FOR EXPERIMENT 2

We compared the density of the neighbourhoods (for all surveys) between the different treatment groups within each addition experiment (early and mid) by repeated-measures ANCOVAs with seedling mass as covariate. The main effect tested was treatment group. Total neighbourhood biomass and neighbourhood biomass/plant at the end of the experiments was compared by ANCOVAs also with seedling mass as covariate. Specific differences between groups were tested with post-hoc contrast analyses at

$p < 0.05$. All statistical analyses for both experiments in 1999 and 2000 were performed with JMP 4.02 (SAS Institute Inc., 2000).

Results

EXPERIMENT 1: SEED ADDITION AND MIMIC

At high water, total plant density was significantly greater in the + *Erodium* pots throughout the growing season (Table I, water \times treatment with additional contrast analyses, $p < 0.01$; Figure 1). The combined addition of *Erodium* and *Erucaria* seeds significantly increased plant density at low but not high water (Figure 1). There was no significant difference between the other treatment groups at each water level. The addition of seeds of the focal species only weakly affected the final plant community; total biomass per plot or mean biomass/plant was not significantly different between the treatment groups (ANCOVAs $p > 0.05$) while number of species was only marginally increased by the addition of *Erodium* seeds (ANCOVA, $F(\text{treatment}) = 2.5$, $p = 0.04$).

The seed bank also had a significant effect on the focal species. *Erodium* sown with seed bank had higher mean germination (and density of *Erodium* throughout season) than *Erodium* sown alone (repeated-measures ANOVA with contrast analyses, $F(\text{treatment}) = 3.3$, $p = 0.039$, $n = 100$, Figure 2). There was no inhibition of *Erodium* germination by *Erucaria* seeds (Figure 2). *Erucaria* germination was, however, strongly inhibited by *Erodium* seeds but unaffected by the general seed bank (repeated-measures ANOVA, $F(\text{treatment}) = 6.1$, $p = 0.0034$, $n = 100$, contrast analyses, Figure 2). There were no significant water \times species interactions ($p < 0.05$).

The density or biomass of neighbourhoods treated with the artificial mimic were not significantly different from the control seed bank in the greenhouse (Figure 1).

EXPERIMENT 2: SEEDLING ADDITION

The addition of *Erodium* seedlings significantly increased the emergence (and density throughout season) from the seed bank if the *Erodium* was planted early in the growing season (Table II with additional contrast analyses, $p < 0.05$; Figure 3a). There was no significant difference between the other additions and the controls (contrast analyses, $p > 0.05$; Figure 3a). *Erodium* seedlings planted early in the season resulted in an increased total density (Figure 3a), total neighbourhood biomass (Figure 3b), and mean neighbourhood biomass/plant (Table III).

Mid-season addition of the three focal species to the germinated seed bank did not have any effect on the density or biomass of the plant community (Figure 3, Repeated-measures ANCOVA and ANCOVA respectively, all $p > 0.05$). *Trifolium* and *Erucaria* did not have significantly different effects (Figure 3).

Discussion

Facilitation has been shown to strongly influence certain plant communities, particularly shrub understorey systems in highly stressed environments (Callaway, 1995). Nonetheless, the central focus of plant ecology has been on

TABLE I. A repeated-measures ANCOVA for plant density throughout the growing season. The different treatments included sowing the 1 \times seed bank without additional seeds, with additional *Erodium* seeds, with additional *Erucaria* seeds, or with an artificial mimic. The covariate was seed mass added.

Effect	df	SS	F ratio	P-value
Model	29	51,570.9	1,778.3	< 0.0001
Census	2	19,685.3	12.9	0.069
Water	1	23,626.2	31.8	0.03
Treatment	4	2,432.5	2.7	0.11
Census \times water	2	1,487.4	3.6	0.028
Census \times treatment	8	1,790.7	1.1	0.37
Water \times treatment	4	2,051.3	2.5	0.04
Census \times water \times treatment	8	746.95	0.45	0.89
Error	569	11,6784.17		

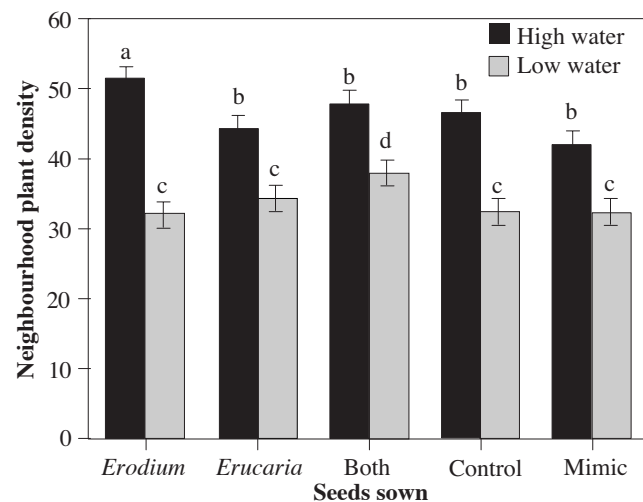


FIGURE 1. The effects of different seed additions, and mimic, on the final total plant neighbourhood density under low and high watering levels. Differences between groups were analyzed with repeated-measures ANCOVA (with contrast analyses at $p < 0.05$ denoted by different letters). *Erodium* and *Erucaria* refer to the seeds added to the 1 \times seed bank.

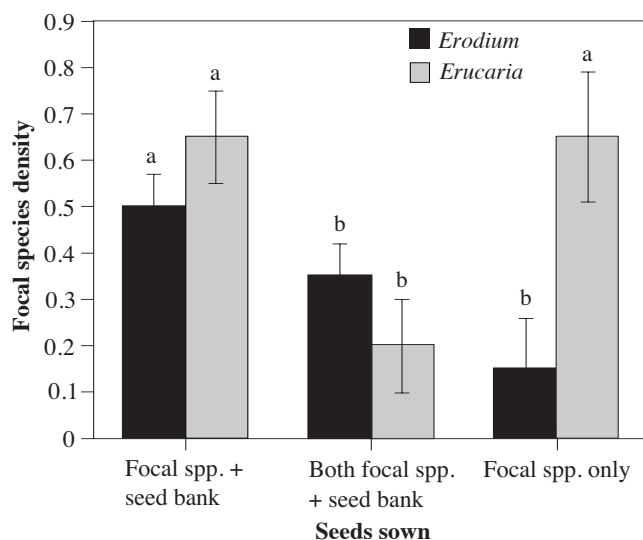


FIGURE 2. The effect of different sowings of seeds of focal species on the mean germination of the focal species (*Erodium* and *Erucaria*). Treatments refer to the identity of focal species added to the seed bank (5 seeds of each species sown). Different letters denote significant contrast analyses ($p < 0.05$).

TABLE II. A repeated-measures ANCOVA for plant density throughout the growing season. The treatments included planting two-week old seedlings (of the focal species) to the seed bank at the start of the growing season. The covariate was mass of seedling planted. Three species of seedlings were added: *Erodium*, *Erucaria*, and *Trifolium*.

Effect	df	SS	F ratio	P-value
Model	7	4753.9	679.1	< 0.0001
Census	1	990	10.9	0.04
Treatment	3	3492.4	12.9	0.03
Census × treatment	3	271.4	2.1	0.1
Error	159	11295.8		

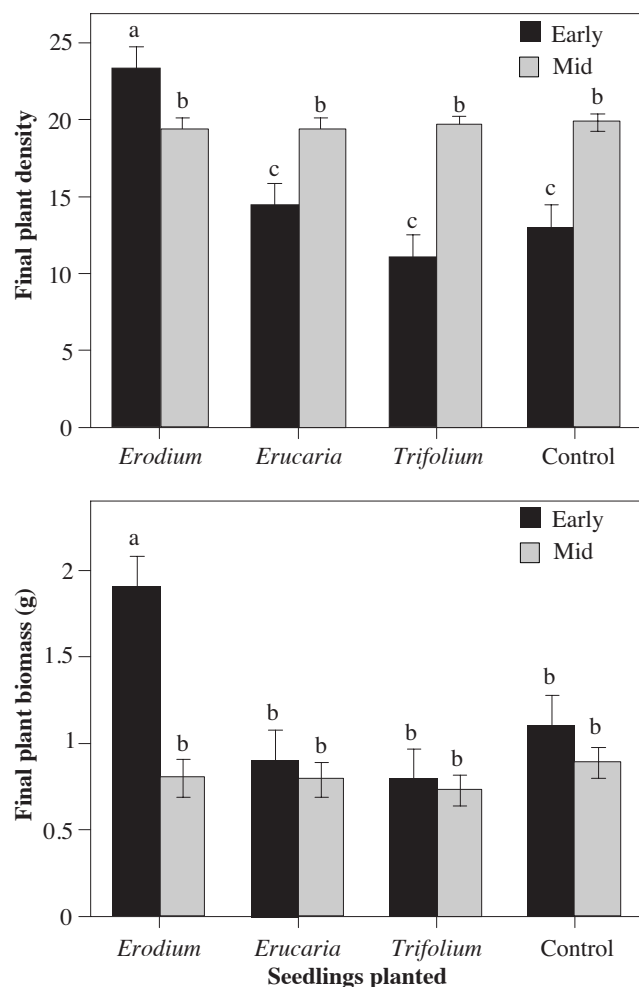


FIGURE 3. Upper panel: The effect of seedling additions of focal species on the total neighbourhood plant density throughout the growing season. Seedlings were added at the beginning of the growing season and mid-season. Lower panel: The effect of different seedling additions on the final total plant biomass of the neighbourhood. Seedlings were added at the beginning of the growing season and mid-season. Different letters denote significant contrast analyses ($p < 0.05$).

testing for and understanding negative plant interactions (Goldberg, 1990). The majority of research on facilitation (outside the context of succession) has been descriptive (Callaway, 1995) while competition studies have largely been experimental, both in the greenhouse (Gibson *et al.*, 1999) and in the field (Goldberg *et al.*, 1999). If we are to develop our understanding of the importance of facilitation

TABLE III. Summary of ANCOVA for total neighbourhood biomass and biomass/plant for the emergent vegetation at the end of the growing season. The treatments were planting two-week old seedlings of the focal species to the seed bank at the start of the growing season. The covariate was mass of seedling planted for three species of seedlings: *Erodium*, *Erucaria*, and *Trifolium*.

Effect	df	SS	F ratio	P-value
TOTAL BIOMASS				
Treatment	3	15.1	8.2	< 0.0001
BIOMASS/PLANT				
Treatment	3	0.017	2.8	0.04

on structuring plant communities, it is crucial to conduct well replicated field experiments and to test for specific species effects (Callaway, 1998). Seed-seed or plant-seed interactions could be extremely important positive effects within plant communities, particularly if positive interactions are more important at earlier life-stages.

In this study, we predicted that the two largest annual plant species, which coincidentally also germinate earlier, influence the entire plant community. The first hypothesis we tested, that the addition of seeds or seedlings of these focal species would increase emergence from the seed bank, was supported for the addition of both *Erodium* seed and seedlings. The additional seeds of this species increased total neighbourhood density throughout the growing season while biomass was not significantly affected. *Erodium* seeds thus had a positive effect on the community. Adding seeds can change the chemical properties of the soil through leachates from seeds or release of CO₂, which subsequently affects the germination of other seeds (Qadir & Abbasi, 1971; Inouye, 1980; Bergelson & Perry, 1989; Murray, 1998). Only two other studies have tested for, and found, a positive effect of adding seeds on subsequent germination of the seed neighbourhood, but both studies focussed on either intraspecific effects (Black & Wilkinson, 1963) or interactions between two species (Bergelson & Perry, 1989). Using pair-wise tests of species of seeds in petri dishes, Qadir and Abbasi (1971) also found many cases of one-way stimulation by a given species of seeds on the germination of another species. Our study is the first to test the effect of specific seeds on a complete community of seeds and measure seed-seed interactions as they influence the final plant community (albeit annuals).

The planting of *Erodium* seedlings had a stronger positive effect on emergence from the seed bank than did the sowing of *Erodium* seeds. This suggests that *Erodium* acts as a nurse-plant for other seedlings rather than through a direct mechanism associated with its emergence, such as breaking the sand crust. Thus, we have a general picture of *Erodium* seeds promoting germination of seeds of other species, and as *Erodium* grows, it continues to have positive effects on the local neighbourhood by acting as a nurse-plant. It would also appear that these effects are specific to *Erodium* since the use of a mimic of the disturbance effect of a large annual germinating did not influence subsequent germination. The effect of *Erodium* seedlings is species specific and not simply a product of some physical perturbation. The shrub nurse-plant effect is well documented in the facilitation literature: possible effects include reduced

water stress, reduced temperature by shading or generating a boundary layer, or increased soil moisture (Callaway, 1995; Pugnaire & Haase, 1996; Callaway, 1998; Holzapfel & Mahall, 1999). Very few studies have tested for nurse-plant effects between herbaceous dicots and grasses. Studies are few, so that no consistent pattern has emerged, but the literature reports examples of positive effects of herbs and grasses on emergence of a second species (Fowler, 1988; Ryser, 1993) and negative effects of established individuals on germination of seed (Ross & Harper, 1972; Shaw & Antonovics, 1986; Bergelson, 1990). While we detected a strong positive effect of *Erodium* seedlings on seed bank emergence, the other tested species (*Erucaria*) had no such effect. Hence, the choice of species is likely important in many systems when testing for interactions between plants. Positive interactions are probably more infrequent and species specific than competitive interactions, making them more difficult to detect (Callaway, 1998). The probability of two species coevolving traits that increase fitness and also benefit another species is significantly less than the probability of simply developing a trait that increases the species' own fitness. In our study system, the small number of species and clear size hierarchy made it easy to select larger focal species; however, further research in more complex systems should also test for positive interactions between herbs and grasses on germination and emergence.

The second hypothesis, that the positive effect of focal species will persist until the end of the growing season, was (generally) supported. The addition of *Erodium* seeds (at high water) and a mixture of *Erodium* + *Erucaria* seeds (at low water) resulted in an increase in plant density until the end of the growing season while the addition of *Erodium* seedlings also increased density, biomass, and biomass/plant. Early positive effects of species on the community can thus strongly influence the final plant community structure in some situations. In a shrub-understorey experiment in the Mojave desert, Holzapfel and Mahall (1999) also reported that the annual plants benefited most from the presence of a shrub early in the growing season. In our study, there was no additional positive effect of adding seedlings to the plants once the seeds had germinated. This is surprising as we expected that there would be some effect, likely interference, of adding larger plants to a mixture of existing plants. The interactions among different species in our community are important early in the growing season because these initial interactions had an influence on the final structure of the neighbourhood. This is comparable to other studies which reported that early asymmetries in plant communities (plants that emerge first are the largest) can be exaggerated in the adult plants (Miller, 1987; Bergelson & Perry, 1989; Gibson *et al.*, 1999). We have demonstrated here that the effect of these asymmetries on the community can be positive. It would be interesting to investigate further what these communities would look like without facilitative effects by selecting high and low density plots and introducing focal species into both. We would predict that the focal species might function positively (facilitation) at lower densities but negatively (competition) at higher densities.

We tested the response of the community at high and low irrigation levels to determine if the effects of focal

species were consistent. We expected that at higher water (lower stress) the effect of focal species would be less than at lower water (high stress) (Bertness & Callaway, 1994). The assumption here was that as stress decreases, the plants increase in size and are more likely to compete and interfere (Bertness & Callaway, 1994). Therefore, we expected that as the level of stress increases in a community, there should be a higher probability of detecting facilitation. This would mean that focal species that act as benefactors to the community reduce abiotic stress and that this effect is more important as stress increases. Our results show that the situation is more complex. We detected facilitation at both irrigation levels, but the effects were not always by the same species, thereby supporting our third hypothesis that the effects of each focal species differ. *Erodium* was the most consistent benefactor species, but abiotic stress may affect the focal species differently from the rest of the plant community. In our system, it is possible that reduced water stress increases the size of the focal species (*Erodium*) and that this increases its ability to facilitate, rather than causing a shift to competition as the general hypothesis would predict (Bertness & Callaway, 1994). We recommend careful use of this framework to predict where facilitation should be most important as focal benefactor species may uniquely respond to stress, which in turn influences the rest of the plant community.

By sowing the seeds of *Erodium* and *Erucaria* independently without seed bank, we tested whether there were effects of the community on the large annuals. The two species were not affected in the same way. *Erodium* had higher germination when a seed bank was present while *Erucaria* was unaffected. *Erodium*, while generally being a benefactor species to the seed bank, inhibited germination of *Erucaria*. This suggests that species interactions are specific and that for *Erodium* there is no cost to being a benefactor species to the greater plant community. In a field-based target-neighbourhood competition experiment (non-manipulative) at the site where we collected the seed, Lessin, Dyer and Goldberg (2001) also found that there was no significant relationship between density or biomass of the neighbourhood and target plant performance (6 target species were tested, including *Erodium laciniatum*). However, the maximum size of target plants was influenced by the neighbourhood, and when the analysis was restricted to the largest target plants, a competitive response was detected (Lessin, Dyer & Goldberg, 2001). This supports our finding that there may be no cost to being a benefactor species but suggests that the net-outcome of the interactions with the community may shift based on benefactor size (or species identity). At least in this simple plant community, experimental manipulation involving the addition of focal species (similar to competition experiments with targets but testing the effect on the neighbourhood instead) provided valuable insight into how facilitation might influence community structure.

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