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Species-specific positive effects in an annual plant community

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Plant facilitation studies commonly test the nurse-plant hypothesis wherein an adult shrub species enhances the establishment of associated herbaceous species under its canopy. Using field and glasshouse experiments, this hypothesis is extended by testing the following four predictions: (1) nurse-plant effects can occur between species with similar life-forms and phenologies (2) positive effects are species specific, (3) the outcome of interactions is life-stage dependent, and (4) facilitative interactions among annuals are primarily commensal. In the Negev Desert in Israel, the response of an annual plant community to removal of relatively larger annuals, *Erodium laciniatum*, *Erucaria pinnata* and *Trifolium tomentosum*, was tested in the field and in the glasshouse. Removal of these dominants was applied early in the growing season, immediately after germination but before establishment of seedlings, and again mid-season following establishment and growth to adults. In both the field and glasshouse, the presence of *E. laciniatum* increased establishment and survival to reproduction of neighbouring plants. These positive effects were life-stage dependent with more positive effects occurring early in the season, and there was no cost of facilitation to *E. laciniatum*. This positive effect was species specific in that neither *E. pinnata* nor *T. tomentosum* had an effect on the plant community. There was also a cost of association with the nurse *E. laciniatum* in that biomass of neighbours was reduced. These experiments demonstrate that the positive effects typically detected at larger scales between species of different life-forms are also occurring at finer spatial scales amongst annuals. This study clearly supports the predictions made in the facilitation literature that effects are species-specific and highly life-stage dependent.

Extensive recent research has demonstrated that facilitation or positive interactions between plants is important in structuring plant communities and informing community theory (Callaway 1995, 2007, Bruno et al. 2003, Lortie et al. 2004, Brooker et al. 2008). The dominant hypothesis tested in the facilitation literature is the nurse-plant hypothesis which proposes that an adult individual of one species enhances the establishment of seedlings of other species within its canopy or immediate neighbourhood, most commonly in a commensal manner with no cost to itself (Niering et al. 1963, Franco and Nobel 1988, Armas and Pugnaire 2005). The most compelling examples of facilitation however include the context dependence of the interactions such as species specificity (Callaway 1998), life-stage dependence (Sans et al. 1998, Sthultz et al. 2007), reciprocity (Pugnaire et al. 1996, Holzapfel and Mahall 1999), environmental gradients (Bertness and Callaway 1994, Holmgren et al. 1997), biogeographical comparisons (Gomez-Aparicio et al. 2004), or size-related effects (Casper 1996, Tewksbury and Lloyd 2001). To further build our understanding of the generality of facilitation in plant

communities, it is necessary to incorporate these concepts into integrated experimental tests for positive interactions.

Here, the scope of the nurse-plant hypothesis is expanded experimentally by specifically testing for annual nurse-plants, using nurse-plant removals, and testing for species-specific effects. While a significant proportion of facilitation studies testing the nurse-plant hypothesis have focused on shrub-understorey systems (Flores and Jurado 2003, Callaway 2007), other studies particularly from salt marshes (Bertness and Shumway 1993, Pennings and Callaway 1996, Hacker and Bertness 1999) and alpine environments (Aksenova and Onipchenko 1998, Arroyo et al. 2002, Cavieres et al. 2002, Kikidze et al. 2005) have studied species with more similar life-forms. However, there are very few examples of positive interactions between annual plants evenly matched in size, life-form, or phenology (Smith 1983, Goldberg et al. 2001, Lortie and Turkington 2002b) and more importantly fewer still incorporating density-dependent interactions within the beneficiary annual species (Lortie and Turkington 2002a).

Arguably, the most common methodological approaches to detecting facilitation include associational surveys (Callaway 1994, Cavieres et al. 2002, Michalet et al. 2002, Armas and Pugnaire 2005) and the addition or transplanting of species into a canopy or an open paired microsite (Levine 1999, Gomez-Aparicio et al. 2004). Nurse-plant

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removal experiments however have the capacity to assess broad community-level effects without the dominant species present (Aksenova and Onipchenko 1998, Estela and Veblen 1998, Holzapfel and Mahall 1999, Olofsson et al. 1999), and this is more tractable in certain life-forms. Furthermore, it has been argued that removal experiments are superior to additions since communities are formed by many processes, not just simple addition, removals inform on the importance of non-random species loss within systems, and indirect, shifting, or unexpected interactions among species is best tested by absence of relative effects and not presence (Diaz et al. 2003). Another advantage of removing species is that it can be applied repeatedly within a growing season or at different times (similar to a natural system with perturbations occurring haphazardly) whereas addition most sensibly is generally limited to seeds or seedlings at the start of a growing season.

Few studies directly test whether positive effects are species-specific by concurrently using other species within a community that could perform a similar function based on life-form, dominance or phenology (Aksenova and Onipchenko 1998, Callaway 1998). Typically, nurse-plants provide shelter that reduces moisture stress (Aguiar and Sala 1999, Pugnaire and Luque 2001) or increases nutrient content (Holzapfel and Mahall 1999, Tirado and Pugnaire 2003) in arid systems. These effects may be substitutable by other species within a community. However, a significant advantage of testing for more than one nurse plant species simultaneously within a community is that this approach provides an assessment of the relative sensitivity of facilitation or net positive outcomes to indirect interactions or the interplay between positive and negative interactions depending on species.

In this study, we explicitly test the importance of facilitation between annual plants with the same life-form and phenology using parallel field and glasshouse target-removal experiments. In both instances, the response of the neighbouring annuals is monitored following removal of larger annual plant species at two different life-stages. In the field, the largest annual species was removed, and in the glasshouse, three different potentially dominant species were tested. This comparative removal design allows a thorough test of the general nurse-plant hypothesis common in many systems but not tested frequently in annuals nor for similar life-forms. Similar to the comprehensive review by Flores and Jurado (2003), we adapt the general nurse-plant hypothesis and assume that in an arid, predominantly annual dune system a slightly larger annual plant species could act as a nurse plant since (1) the literature inspected in this review frequently detected this specific form of facilitation, i.e. differential seedling establishment with no cost to the benefactor, and (2) that nurse plants may not be restricted to shrubs or particular taxa. We use this generalized nurse-plant hypothesis as a starting point but will extend its scope by testing the following predictions:

1. *Benefactor effect.* Some annual plant species can function as nurse-plants and increase the establishment, survival, or mean plant size of its immediate neighbours.

2. *Species specificity.* Positive effects are species specific, i.e. difference in size between plant species does not necessarily ensure that the larger species will act as a nurse-plant.
3. *Life-stage dependency.* The outcome of interactions is life-stage dependent, and the potential effect of a nurse-plant will vary within a growing season.
4. *Commensal interactions.* The neighbourhood or associated plants within a patch will not influence the performance of the larger nurse-plant.

Additionally, neighbourhood density (Goldberg et al. 1999), environmental 'stress' (Bertness and Callaway 1994), and benefactor size (Tewksbury and Lloyd 2001) are proposed as important drivers of facilitative interactions in many studies and as such are similarly tested in this study as potential modifiers of plant-plant interactions.

Methods

Study site and species description

The study site is a semi-stabilized sand dune dominated by winter annuals and sparsely distributed shrubs, the *Artemisia monosperma* and *Stipagrostis scoparia* associations (Orshan and Zohary 1963) at Bir Asluj in the Holot Mashabim Nature Reserve (31°00'212'N, 34°44'474E) in the central Negev desert, Israel. There are approximately 20 species of annual plants in this community (Dyer et al. 2001, Goldberg et al. 2001). Rainfall occurs primarily in the winter months (December to April) and has a 30 year average of 110 mm per year (Goldberg et al. 2001). The field experiment was done on the south face of a dune with prevailing winds from the northwest. The bottom of the dune has lower temperatures and higher soil moisture than the top of the dune, spanning a linear 50 m elevational gradient (Lortie and Turkington 2002a).

Field experiment

A 2 × 2 factorial design was used to test for facilitative annual-annual nurse-plant effects including (1) two removal times – early season immediately after germination but before establishment, and mid-season once plants had established and (2) two positions on the stabilized sand dune, the upper and lower dune corresponding to more and less harsh environmental conditions respectively (Lortie and Turkington 2002a). *Erodium laciniatum* was selected for the field study because it is commonly the largest annual (erect to about 40 cm), is one of the first to germinate (Lessin et al. 2001), and has been shown to have positive effects under controlled conditions on neighbouring annual plants (Lortie and Turkington 2002b). We recorded the relative effects of removal of *E. laciniatum* on the neighbourhood and the effects of the neighbourhood on intact *E. laciniatum* individuals in control plots. Successive measurements of density and number of species were taken throughout the growing season to track relative survival.

On 12 January 2000, after early rains when most of the seedlings had emerged, two parallel 100 m transects were placed on the dune – one at the top and a second at

the bottom. On each, we selected 120 pairs of similarly-sized *E. laciniatum* that were between 0.75 and 1 m apart. The number of leaves of *E. laciniatum* were measured at this time and tested for differences within pairs. A 15 cm diameter ring was centered on *E. laciniatum* to record neighbourhood density and ensure that density was not significantly different within pairs at the onset of the experiment. A neighbourhood size of 15 cm conservatively samples the maximum sphere of influence by an annual plant of this size (Mack and Harper 1977), and hereafter is referred to as the immediate neighbourhood.

After the initial measurements, 60 pairs of *E. laciniatum* per transect were randomly assigned to one of two removal times – early or mid-season, and within each pair, one plant was randomly assigned to control or removal. *E. laciniatum* were removed on either 12 January or 3 March by gently pulling it out of the sand. The sand on the dune is loose with no crust, and the removal treatment did not significantly disturb the sand any more than wind or other natural disturbances. The importance of artificial fine-scale sand disturbance has been previously tested in this system and had no relative effects on the immediate plant community (Lortie and Turkington 2002b).

The number of leaves of *E. laciniatum* and the density of the immediate neighbourhood of the target was recorded every two weeks – six times for the early season removals and three times for the mid-season removals. At the final census (15 April 2000), all aboveground biomass was collected from the neighbourhoods. Control *E. laciniatum* plants were also harvested (aboveground). All plants were dried at 60°C for 48 h and weighed.

Potential reciprocal effects of the neighbourhood on *E. laciniatum* were tested using (1) the experimental control plots with *E. laciniatum* present and intact and (2) an additional 60 *E. laciniatum* on each transect that were naturally growing without neighbours in its immediate neighbourhood. The number of leaves and width of canopy for these *E. laciniatum* were measured and these targets were similarly harvested, dried and weighed.

Glasshouse experiment

Seeds for the glasshouse experiment were also collected at the site in November 1999. We collected the top 2 cm of sand which effectively samples at least 99% of the total seed bank, and a 500 µm sieve removes all the seed from the sand (Goldberg et al. 2001). The natural seed bank density, calculated for the field site, is 600.8 g m⁻² (Lortie and Turkington 2002a, 2002b). The experiment was done in an open air glasshouse at the Mitrani Dept for Desert Ecology Research; 25 km southeast of the site where seed was collected. We chose three common species from the local plant community as target species for removal in the glasshouse study; *Erodium laciniatum* (largest annual), *Erucaria pinnata* (another of the larger annuals also up to 40 cm tall), and *Trifolium tomentosum*, a leguminous annual (up to 15 cm tall) (Lessin et al. 2001).

Seeds were planted on 4 January 2000 in 15 cm diameter pots filled with sterile, seedless sand excavated from a 10 m deep commercial quarry. The planting density of the seed bank was equivalent to the natural seed density

in the field, i.e. 6 g of seed per 10 × 10 cm surface area. A buffer strip of 4.5 cm was designated in each pot to minimize edge effects. Pots were watered every 10 days throughout the growing season to an equivalent of 150 mm mean annual precipitation. The pots were surveyed once each week for the first three weeks to determine emergent plant density and to select replicates for the experiment. A total of 600 pots were sown with seed, and from these, the following groups were selected: mixtures with all three target species absent, and mixtures with only one of each of the three target species present.

The target-plant removal design (described in 'Field experiment') was applied to half the replicates for each species (using a randomized block-design). Target species were removed early season post-germination on 27 January or mid-season on 5 March 2000. There were 40 replicates per treatment group for each target species in the early removal pairs and 20 pairs per species mid-season for pots with *E. laciniatum* and *T. tomentosum* but not for pots with *E. pinnata*. Unfortunately, there was significant mortality in *E. pinnata* pots designated for mid-season removal and sample size was too reduced for inclusion in the analyses.

The density of the neighbourhood, number of species, and number of leaves of target species were recorded at successive censuses following emergence, and on 17 April 2000 all plants were clipped at ground level and above-ground material collected. Target species in control pots were harvested separately. All plants were dried for 48 h at 60°C and weighed.

In both experiments, the end-date was determined by natural phenology, i.e. when the majority of species within plots had flowered and begun to set seed. Due to the extremely small size of most individual plants and seeds, neither seed collection nor biomass per species were tractable.

Analyses

Benefactor effects

The relative effect sizes of target plant removal on its immediate neighbourhood was estimated by calculating the 'relative interaction index' or Rii (Armas et al. 2004) for establishment, survival, and biomass of the plants within plots/pots in both experiments. This index effectively compares performance of the neighbourhood 'with' and 'without' the target species and is calculated as follows:

$$R_{ii} = (C - T)/(C + T)$$

The target species present within the neighbourhood is denoted by C and treatment neighbourhoods with target removed are indicated by T. Rii is an appropriate metric to compare presence/absence experimental designs as it is symmetric around 0, normalized, and ranges from -1 to +1 with negative values indicating competition and positive values indicating facilitation (Armas et al. 2004). Two-tailed t-tests were used to determine if each effect mean size estimate, Rii, was significantly different from no effect (a value of 0) at p < 0.05 (Hedges et al. 1999).

Establishment was calculated as the proportional change in density from the census at the time of application of the treatment to the subsequent census post-application, two weeks later. Survival was calculated similarly for each census period including at the termination of each experiment, and

mean plant size was also calculated for the final census. To conceptually clarify, establishment refers to the phenological point within this annual plant community when no additional germinants were detected, and the survival estimate primarily discussed herein refers to the proportion of individuals within a plot that reached reproductive maturity. The number of species in the immediate neighbourhood was also explored but did not significantly respond to removal, vary by experiment, nor negatively impact the target species. As such, only the three primary measures will be reported herein.

Species specificity and life-stage dependency

Species specificity and life-stage dependency was tested for the glasshouse experiment by comparing the Riis for each response variable using a two-way ANOVA with target species and experimental removal time as main effects. Life-stage effects were also tested in the field experiment by comparing removal-time effects on the Rii for responses with a one-way ANOVA. To more precisely explore life-stage changes within the communities, survival to each subsequent census was tested with a repeated measures ANOVA for each experiment with appropriate post hoc contrast analyses (Tukey HSDs).

Commensal interactions

The reciprocal effect of neighbourhood plants on the number of leaves, width and biomass of *E. laciniatum* was tested using regression analyses of neighbourhood density, total neighbourhood biomass, or mean neighbour biomass as independent variables in both experiments. Following Lessin et al. (2001), we applied a boundary constraint approach to the neighbourhood biomass and regressed these values against the proportion of maximum *E. laciniatum* biomass within each width class for a range of different classes. The size of *E. laciniatum* plants naturally found without neighbours and those in the control plots was compared using ANOVA.

Density, environmental stress and benefactor size

In both the field and glasshouse, neighbourhood plant density was free to vary when treatments were imposed. As such, the density of the plants within each experimental plot/pot was tested via ANCOVA with treatment, neighbourhood density and interaction effects for each response variable. Net differences in density between pairs of control and treatment plots at the completion of experiments was tested as a predictor of effect size (Rii). Regression analyses were also used to test for density-dependence by exploring slope and shape of fit (Goldberg et al. 2001). Total plant densities between the two experiments, field and glasshouse, were compared using a two-way ANOVA for experiment and treatment for *E. laciniatum* treatments.

The stress-gradient hypothesis was tested by comparing the relative effects of *E. laciniatum* at the two dune positions in the field experiment via two-way ANOVAs with interaction effects for each response variable. Additionally, benefactor size as a modifier of plant–plant interactions was explored via regression analyses of target-plant size (number of leaves, width, and final biomass) on neighbourhood

establishment, survival and mean plant neighbour size. These analyses were repeated for both early and mid-season removals in field and glasshouse.

Statistical considerations

The potential for inflated type II errors was assessed by repeated measure MANOVAs and MANCOVAs within each experiment for the three primary response variables tested including establishment, survival, and mean plant size. This approach ensures that the significant main effects reported in each ANOVA, t-test, or regression are not the artifacts of multiple testing (Huberty 1989, Marcheselli 2002). We did not detect false positives for main effects reported in any instance, and accordingly simple statistics are reported. Homoscedasticity and normality were assessed and appropriate transformations applied – census-to-census survival was arcsine square-root transformed (Sokal and Rohlf 2003), but back-transformed values are reported throughout. Experimental treatment and species were modeled as fixed effects while census was modeled as a random effect. Between experiment comparisons of effect sizes were explored using the data exploration tools of MetaWin 2.0 including normal quantile plots and calculation of weighted means for each response variable effect size (Rosenberg et al. 2000), however too few instances of independent tests were done for a full meta-analysis. All statistics reported were done using JMP 7, SAS 2007. When a series of multiple tests are summarily reported in parentheses below, the notation all ‘p > listed value’ reports the lowest p-value detected in the series of tests.

Results

Benefactor effects

The presence of *E. laciniatum* positively influenced the relative establishment and survival to reproduction in both the early and mid-removal plots in the field and in the early removal treatments in the glasshouse (Table 1, Fig. 1, 2a). Neighbourhood biomass (mean plant size) was also increased by the presence of this target species in the field in the early removals but had either no effect mid-season in the field or early season in the glasshouse, or strongly negative effects on mid-season plots in the glasshouse (Table 1, Fig. 1, 2a).

The removal of *E. pinnata* had no effect on establishment or survival to reproduction but negatively impacted final neighbourhood biomass (Table 1, Fig. 2b). The smallest target annual tested, *T. tomentosum*, had no relative effect on any Rii when removed early in the experiment but had significant negative effects on establishment and neighbourhood biomass when present in pots mid-season (Table 1, Fig. 2c).

Species specificity

In the glasshouse experiment, the effects of target species on the immediate neighbourhood were highly specific with both sign and magnitude of effect varying significantly by species for all three interaction indices (Table 2 contrasts).

Table 1. Summary of analyses testing the relative effect of target-species removal on the immediate plant community. The response is calculated using the response ratio R_{ii} . Experimental removal of the larger annual (*Erodium laciniatum*) was done in the field and glasshouse (one and three species tested respectively) and three measures were tested. Significant p-values are in bold, and sign indicates whether the relative effect of the target species presence was positive, negative, or neutral.

Experiment	Removal	Target	Measure	DF	t	p	Sign
Field	Early	<i>Erodium laciniatum</i>	establishment	52	5.75	0.0001	+
			survival	52	2.9	0.005	+
			biomass	52	4.1	0.0002	+
	Mid-season	<i>Erodium laciniatum</i>	establishment	37	2.89	0.0064	+
			survival	37	3.22	0.0026	+
			biomass	37	-0.55	0.58	0
Glasshouse	Early	<i>Erodium laciniatum</i>	establishment	19	4.05	0.0007	+
			survival	19	5.25	0.0001	+
			biomass	19	-1.6	0.12	0
	Mid-season	<i>Erodium laciniatum</i>	establishment	13	-0.73	0.48	0
			survival	13	2.13	0.05	+
			biomass	13	-131.7	0.0001	-
	Early	<i>Erucaria pinnata</i>	establishment	19	0.96	0.35	0
			survival	19	1.1	0.29	0
			biomass	19	-4.1	0.0006	-
	Early	<i>Trifolium tomentosum</i>	establishment	19	0.2	0.85	0
			survival	19	-0.45	0.66	0
			biomass	19	-1.94	0.068	0
	Mid-season	<i>Trifolium tomentosum</i>	establishment	18	-11.9	0.0001	-
			survival	18	-0.88	0.39	0
			biomass	18	-69.9	0.0001	-

On average, *Erodium laciniatum* had significantly different effects on establishment and survival to reproduction relative to the other two target species (Table 2). The magnitude of the mean positive effect on establishment by *E. laciniatum* was approximately half the mean negative effect of the other two species (*E. laciniatum*: $R_{ii\text{establishment}} = +0.05 \pm 0.03$, *E. pinnata*: $R_{ii\text{establishment}} = -0.11 \pm 0.04$, and *T. tomentosum*: $R_{ii\text{establishment}} = -0.17 \pm 0.03$) while the positive survival effects of *E. laciniatum* on its neighbourhood were three to five times greater in magnitude than the other targets (*E. laciniatum*: mean $R_{ii\text{survival}} = +0.21 \pm 0.06$, *E. pinnata*: mean $R_{ii\text{survival}} = +0.04 \pm 0.09$, and *T. tomentosum*: $R_{ii\text{survival}}$

$= -0.065 \pm 0.06$). However, all three target-plant species had significant negative effects on biomass of the neighbourhood with *E. pinnata* having the most negative mean effect early season (Table 2 with post hoc contrasts).

Life-stage dependency

The experimental removal of target-plant species at two life-stages significantly differed for the overall establishment and biomass of the neighbourhoods in the glasshouse with early experimental treatments positive in sign, i.e. presence of target is positive, while mid-season removals were negative in sign, i.e. presence had a negative effect on neighbourhood (Table 2). In the field experiment, only biomass of the neighbourhood responded differently to *E. laciniatum* removal at different life-stages with early removal eliciting a greater response (ANOVA, $F_{1,1} = 8.82$, $p = 0.0038$; Fig. 1). The more precise life-stage dependency analyses using census-to-census survival estimates detected significant temporal effects of census in all instances but no significant interaction effects by treatment (Table 3). In both experiments at both removal times, survival significantly decreased in the census immediately following treatments (Table 3, Tukey HSD post hoc contrasts).

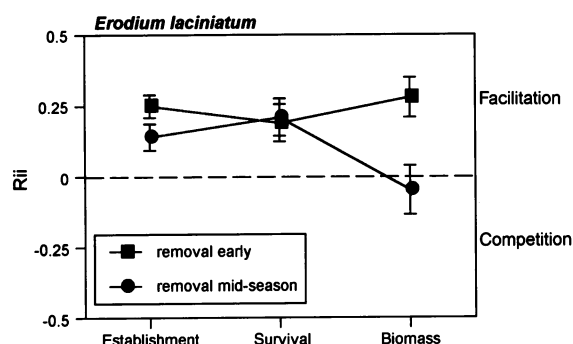


Figure 1. The mean (± 1 SE) relative interaction indices (R_{ii}) for establishment, survival to reproduction, and biomass of the immediate neighbourhoods associated with *E. laciniatum* control and removal plots in the field. Establishment is the relative number of individuals that persisted following treatment (either *E. laciniatum* present or removed at two life-stages), survival is the relative number of individuals present at the completion of experiment reaching reproduction, and biomass is the mean number of individuals present by total density. Positive values indicate facilitation by the presence of the target species and negative values indicate release from competition by removal of the target species.

Commensal interactions

In the *E. laciniatum* controls plots, neither neighbourhood density nor total neighbourhood biomass influenced the number of leaves, width, or final mass of this target-plant species in the field or glasshouse (regression analyses, all $p > 0.2$). There was also no significant difference between *E. laciniatum* grown with and without neighbours naturally in the field (ANOVA comparing the supplemental field plots free of neighbours to control plots in early and mid-removal pairs, $F_{2,2} = 0.7$, $p = 0.5$). The boundary

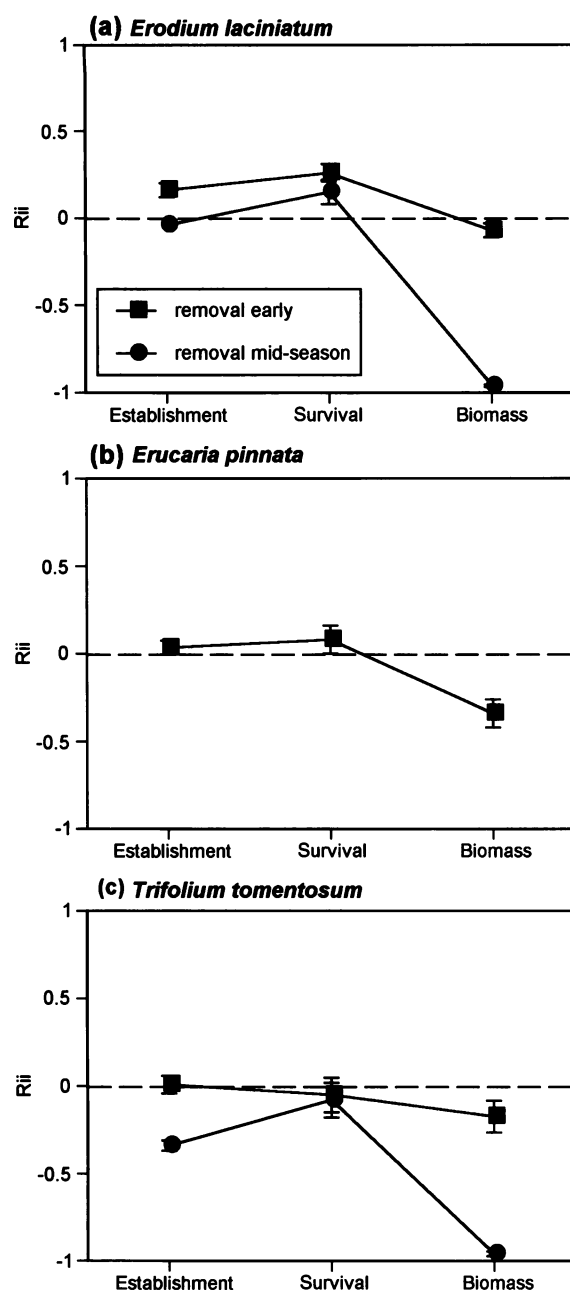


Figure 2. The mean (± 1 SE) relative interaction indices (Rii) for establishment, survival to reproduction, and biomass of the immediate neighbourhoods associated with the removal of three species. Two removal times were tested: early in the season following germination but preceding establishment of seedlings and mid-season once neighbouring annuals established as adult plants. Positive values indicate facilitation by the presence of the target species and negative values indicate release from competition by removal of the target species.

constraint analysis of neighbourhood biomass did not significantly predict *E. laciniatum* mass (regression analyses, all $p > 0.19$).

Density, environmental stress and benefactor size

At the initiation of the experiments for both the early and mid-season removals, there were no significant differences

in the density of plots/pots nor the size of the target plant removed (ANOVAs, all $p > 0.08$). There were significantly more plants in the glasshouse experimental communities relative to the field experimental plots at the completion of the experiments (ANOVA, $F_{1,3}$ experiment = 156.4, $p = 0.0001$; means = 17 ± 0.73 and 6.25 ± 0.45 respectively) but there was no significant treatment \times experiment interactions. The density of the local neighbourhood within plots did not significantly interact with treatment effects on any response variable in either experiment (ANCOVAs, all treatment \times density interactions $p > 0.08$). However, the difference in final plant density between pairs of control and treatment plots of *E. laciniatum* targets in the field and glasshouse significantly predicted Rii survival with greater differences in density relating to more positive values of Rii (Fig. 3; all $p < 0.01$, $r_{\text{field early}}^2 = 0.57$, $r_{\text{field mid}}^2 = 0.33$, $r_{\text{glasshouse early}}^2 = 0.54$, and $r_{\text{glasshouse mid}}^2 = 0.39$). Rii establishment and biomass were not related to the differences in density between the *E. laciniatum* control and treatment plots (regression analyses, all $p > 0.06$).

An effective stress gradient was detected in general with significantly lower densities of the unmanipulated plant communities at the top of the dune (abiotically more harsh) relative to the bottom of the dune (ANOVA, $F_{1,51} = 28.6$, $p = 0.0001$; i.e. on average 20% less plants within plots at the upper dune position), and additionally, individuals of *E. laciniatum* used as procedural controls, i.e. without neighbours and unmanipulated, weighed significantly less at the end of the growing season at the top of dune relative to the lower dune position (ANOVA, $F_{1,34} = 5.8$, $p = 0.02$). In spite of the evidence for a stress-gradient, dune position did not significantly influence the relative effects of *E. laciniatum* removal on Rii establishment, survival to reproduction, or biomass of the neighbourhood under either early or mid-season treatments (ANOVAs, all $p > 0.2$). Target-plant size (width, number of leaves and final biomass) did not significantly predict the intensity or sign of the three relative interaction indices tested for either experiment, target species, or removal time (regression analyses, all $p > 0.3$).

Discussion

Here, we test whether a relatively larger annual plant species can have a significant positive effect on smaller annuals similar to shrub nurse-plants in other systems (Niering et al. 1963, Franco and Nobel 1988, Armas and Pugnaire 2005). We also test whether these effects are specific (Callaway 1998), life-stage dependent (Tielborger and Kadmon 2000b, Stultz et al. 2007), and whether the associated smaller annuals in the system reciprocally affect the target species (Pugnaire et al. 1996, Holzapfel and Mahall 1999). The generalized version of the nurse-plant hypothesis proposed in this study was supported in that a larger annual plant with similar phenology and life-form facilitated the relative establishment and survival of associated plant species.

The detection of a nurse-plant syndrome amongst annuals is important. First, only the largest annual in the system acted as a nurse-plant, and not for all response measures, which suggests that positive effects in this arid,

Table 2. Summary of ANOVAs testing for species specificity and experimental removal time in the glasshouse target-plant removal experiment. Rii refers to the relative interaction index calculated for each response variable including the establishment of the immediate plant neighbourhood, survival to reproduction, and biomass. Significant p-values are in bold, and 'contrast' refers to Tukey HSD post hoc contrast analyses at $p < 0.05$ for species contrasts. Levels not significantly different from one another are reported jointly in square parentheses, and abbreviations are as follows: Ero = *E. laciniatum*, Eru = *E. pinnata*, and Tri = *T. tomentosum*. The contrasts indicated in the removal rows indicate sign of mean effect size (i.e. only two levels so no formal contrasts needed).

Rii	Factor	DF _{num}	DF _{den}	F	p	Contrasts
Establishment	Removal	1	3	42.7	0.0001	Early (+) Mid (–)
	Species	2	3	12.99	0.0001	Ero [Eru, Tri]
Survival	Removal	1	3	0.68	0.42	n.s.
	Species	2	3	3.39	0.0062	Ero [Eru, Tri]
Biomass	Removal	1	3	170.75	0.0001	Early (+) Mid (–)
	Species	2	3	4.5	0.014	[Ero, Tri] Eru × Early

annual plant community are species specific. This pattern supports the infrequently tested hypothesis proposed by Callaway (1998) that positive effects can be highly specific. Second, the most common conceptualization of the nurse-plant hypothesis and empirical tests thereof rely on the adult life-stage of the nurse-plant species to enhance the establishment of seedlings of other species (Armas and Pugnaire 2005, Maestre et al. 2005, Brooker et al. 2008). Here, positive effects were detected amongst species sharing similar phenologies and life-stage transitions, and further, experimental imposition of treatment at different times also detected an interaction shift from positive to negative in the case of the largest annual, *E. laciniatum*. Hence, nurse-plant effects can occur pre-establishment between seedlings. Third, similar to nurse-plant studies including estimates of reciprocity within the associations (Holzapfel and Mahall 1999, Flores and Jurado 2003), the set of interactions detected can be commensal since the smaller annuals did not significantly affect either the two larger annual target species nor the third smaller annual target. This set of shifting positive/neutral interactions in both the field and

greenhouse not only supports the previous nurse-plant studies (Callaway 2007) but demonstrates the sensitivity of net interactions to species within the community (Gaucherand et al. 2006, Brooker et al. 2008).

Interactions between species are best viewed as an interplay between competition and facilitation (Callaway and Walker 1997). Recent studies on facilitation in particular have considerably furthered our understanding of how this interplay might shift through time (Brooker and Callaghan 1998, Tielborger and Kadmon 2000b) or along gradients (Bertness and Yeh 1994, Pugnaire and Luque 2001, Tewksbury and Lloyd 2001). However, the measure used to estimate relative effects might also introduce an element of sensitivity to whether positive or negative net effects are inferred (Travis et al. 2006), and while this may seem like a limitation, it is advantageous as it provides another means to assess interplay. In this system, we conclude that *E. laciniatum* serves as a nurse-plant and benefits its neighbours in both the field and greenhouse. However, not all instances tested generated a net positive effect. The presence of this target species had a large and

Table 3. Summary of repeated measure ANOVAs for survival to each census calculated as the relative change in density from the previous sampling event. Experimental removal of the larger annual was done in the field and glasshouse (one and three species tested respectively) and treatment is thus removal, target intact, and in some instances also included a procedural control (i.e. target naturally absent). Significant p-values are in bold, and 'contrast' refers to Tukey HSD post hoc contrast analyses. However, only the census immediately following treatment was significantly different from others and the p-value is reported for this contrast. The contrasts reported as 'na' indicate that there were only two levels for that effect so no contrast was needed.

Experiment	Removal	Target	Effect	DF _{num}	DF _{den}	F	p	Contrast
Field	Early	<i>E. laciniatum</i>	Treatment	1	7	19.1	0.0001	0.014
			Census	3	7	25.7	0.0001	
			Tr. × Cen.	3	7	1.68	0.17	
	Mid-season	<i>E. laciniatum</i>	Treatment	1	5	5.38	0.021	0.002
			Census	2	5	12.7	0.0001	
			Tr. × Cen.	2	5	1.04	0.36	
Glasshouse	Early	<i>E. laciniatum</i>	Treatment	2	8	7.45	0.0008	0.0001
			Census	2	8	23.69	0.0001	
			Tr. × Cen.	4	8	0.12	0.98	
	Mid-season	<i>E. laciniatum</i>	Treatment	1	3	36.66	0.0001	na
			Census	1	3	14.69	0.0003	
			Tr. × Cen.	1	3	0.49	0.4845	
	Early	<i>E. pinnata</i>	Treatment	1	5	0.115	0.7355	0.0001
			Census	2	5	18.4	0.0001	
			Tr. × Cen.	2	5	0.067	0.94	
	Early	<i>T. tomentosum</i>	Treatment	1	5	0.145	0.7	0.0001
			Census	2	5	32.74	0.0001	
			Tr. × Cen.	2	5	0.74	0.48	
	Mid-season	<i>T. tomentosum</i>	Treatment	1	3	60.16	0.0001	na
			Census	1	3	25.36	0.0001	
			Tr. × Cen.	1	3	6.29	0.014	

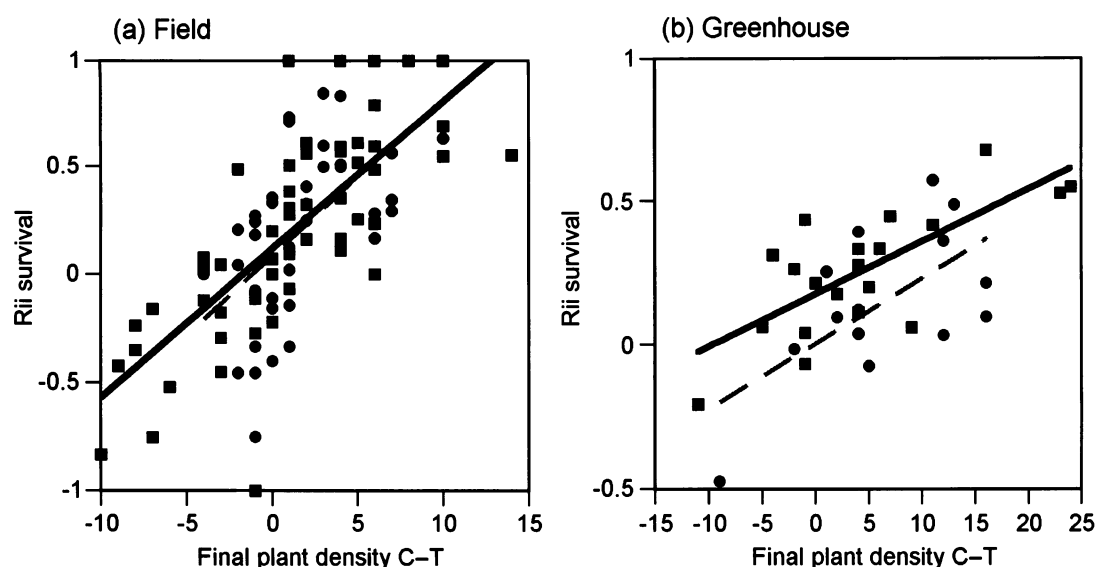


Figure 3. Regression analyses of the effect of paired-differences in plant density between control (C) and removal plots (T) for the target species *E. laciniatum* on the relative survival (Rii) of the annual plants in the immediate neighbourhood. The experiment was repeated in the field and glasshouse at two time intervals (early in the growing season: square symbols with solid line and mid-season removals: closed circles with dotted fit line). Fitted lines are significant at $p < 0.01$ and $r^2 > 0.3$.

significantly negative effect on biomass of the neighbourhood relative to its absence mid-season (while in the field its relative removal effect mid-season was neutral). Hence, under some conditions the absence of a nurse-plant can release associated species from competitive interactions at later life-stages (Walker 1994). Facilitative nurse-plant interactions can thus come at a cost to annuals since seed set is highly correlated with biomass (Miller 1987) and annuals are subject to significant tradeoffs within character sets associated with both vegetative final mass and length of time to grow (Aarssen and Jordan 2001). Arguably, the early positive effects of *E. laciniatum* on establishment and then on final neighbourhood-level survival are at least as important since without those positive effects, many of the individuals would not persist to reproduction, albeit perhaps reduced. The presence of this cost only in the glasshouse with mid-season removal suggests that the relatively favourable conditions generated in terms of available soil moisture, reduced sand abrasion effects, etc. can shift the interactions from positive or neutral in the field (i.e. natural conditions) to negative when plant densities are increased (glasshouse > field plots) and environmental limitations reduced. However, variation in stress within the natural field conditions did not modify the positive effect of *E. laciniatum* which suggests that either this specific gradient, albeit different in community density and environmental conditions, still did not encompass a wide enough range of variation in stressors or that the stress-gradient hypothesis best describes broader patterns (Bertness and Callaway 1994).

To the best of our knowledge, few studies have experimentally tested and detected direct annual-annual nurse-plant facilitation (Aksenova and Onipchenko 1998, Lortie and Turkington 2002b). The former study removed five dominant species from alpine tundra over a period of 13 years and found both positive (91 instances) and negative (85 instances) responses by the vegetation depend-

ing on the species removed. In the latter study, potential effects by the same three dominant plant species in this study were tested in the glasshouse by adding seeds or seedlings to the seed bank. Species-specific positive effects were also detected with *E. laciniatum* facilitating increased neighbourhood density (Lortie and Turkington 2002b). Similar to both the field and glasshouse experiment in this study, the largest positive effects occurred at earlier census intervals. In contrast, there was no evidence of a shift to negative interactions or costs to the immediate neighbourhood in associating with the three dominant annuals added experimentally in the glasshouse at later life-stages compared to the glasshouse study here testing for interactions via removals (Lortie and Turkington 2002b). Competitive effects were significant in the glasshouse target-removal experiment with the negative effect sizes sometimes several times greater in magnitude than positive effects. This supports the empirical research for similar systems in which diffuse competition can play a significant role in determining community structure (Fowler 1986, Tielborger and Kadmon 2000a, Pugnaire and Luque 2001) while recent theory development has proposed that indirect plant-plant interactions may be transitive and common in complex systems (Brooker et al. 2008). Additionally, Diaz et al. (2003) have proposed that removal experiments are more powerful in their capacity to detect diffuse interactions and this study supports this assertion. In combination, these studies suggest that in arid and alpine annual plant communities, the presence of a dominant annual species can significantly influence the outcome of the interaction between species within the community at small-scales and that these shifts are both species specific and sensitive to measure tested and experimental method.

While the effects of the nurse-plant *Erodium laciniatum* in this annual plant community were detectable in the field and greenhouse via removal and addition, no specific mechanism was identified. However, several explanations

are possible. In selecting two additional annuals, we not only tested whether the positive effects were species-specific but also coarsely explored potential mechanisms. If positive effects were strictly a product of physical shelter (Carlsson and Callaghan 1991), then it is surprising that the second largest annual *Erucaria pinnata* did not produce a positive effect. The common smaller annual species *Trifolium tomentosum* also had the capacity to generate positive effects on the plant community via nitrogen fixation but did not act as a nurse-plant. Admittedly, these are very coarse tests for mechanism but do suggest that facilitation is not directly related to plant size or nutrients. Furthermore, tests within *E. laciniatum* for importance of width, number of leaves, or target plant biomass did not significantly predict the magnitude of positive effects on establishment or survival. Thus, the positive effects are related to presence of the species and not variation in the size of the adult which is reasonable since the positive effects can occur very early in the growing season. Interestingly, the most likely explanation may be a combination of various direct and indirect effects associated with the presence of annual species which germinate earlier.

The positive effect of a larger annual plant was more important early in the growing season, and removal effects may persist throughout the growing season by increasing survival. A growing body of literature supports the prediction that facilitation is more important early in the life-stage of plants (Callaway and Walker 1997, Holzapfel and Mahall 1999, Brooker et al. 2008). Seedlings are more sensitive to abiotic stress (Foster 1999), and as plants grow, it is more likely that they will interact negatively via interference or competition for resources (Callaway and Walker 1997). This study explicitly tested when the positive effect occurred by successive measurements and by removing the target-plant species at different times. Few studies test the importance of interspecific interactions by incorporating these approaches experimentally (Diaz et al. 2003), and it has been proposed that accurate assessment of outcome versus dynamics requires successive measurements, field and greenhouse comparison, and expansion beyond pair-wise mixtures (Gibson et al. 1999, Connolly et al. 2001). Combined with the previous addition experiment (Lortie and Turkington 2002b) and tests for net interactions via changes in the initial community density (Goldberg et al. 2001, Lortie and Turkington 2002a), interactions within an annual community early in the growing season between seedlings sets the conditions, and perhaps determines to an extent, final outcomes.

The three dominant annuals tested in this system were not influenced by the immediate neighbourhood of annual plants. The nurse-plant effect detected in this annual plant community was commensal, and the net competitive effects were asymmetric. Lessin et al. (2001) also reported no significant relationship between target performance and density or biomass of the neighbourhood for six species of annuals including *E. laciniatum*. However, they detected negative effects of the size-class restricted biomass of the neighbourhood on the maximum size of target plants within each class. We did not detect significant effects using this approach, and as such conclude that there is limited evidence for direct interactions between the domi-

nant annuals and the other annual species within the plant community in this arid system. Additional tests for interactions via density dependence within this study further supports the conclusion that smaller annuals weakly interact and do not influence the dominants. Density of the neighbourhoods did not interact with the effects of the dominant species, and more importantly, the relative difference between the densities of control and treatment plots for *E. laciniatum* either did not predict emergence and biomass of the neighbourhood or positively predicted the survival to reproduction of the associated species. Thus, increasing density within plots did not increase the likelihood of negative interactions with the nurse-plant species.

Conclusions

The general nurse-plant hypothesis was supported for an arid, annual plant community. Positive effects were species specific, life-stage dependent, and restricted to the largest annual plant species in the community. The presence of detectable complex interactions at this fine scale offers a unique opportunity experimentally as it is amenable to both thorough density and target species manipulations and also from a theory development perspective as indirect interactions are highly likely. While this study focused primarily on testing for a nurse-plant effect, competition and possibly release from its effects by co-dominant species was important in determining some measures of neighbourhood-level success and a prevalent interaction in addition to facilitation. Strengths of this study include successive measurements, experimental manipulation at different life-stages, field and greenhouse tests, and the effects of several potential nurse-plant species on the immediate, natural assemblage of species.

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