COMMUNITY ECOLOGY

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Shrub spatial aggregation and consequences for reproductive success

Abstract To link spatial patterns and ecological processes, we analysed the distribution of two shrub species (one large and dominant, the other smaller) and estimated the reproductive consequences of their distribution for the smaller species. We tested the significance of the spatial distribution pattern of the two shrubs by second-order bivariate point pattern analysis (Ripley's K function). Performance of *Asparagus albus*, the smaller shrub, was measured as (1) survival of transplanted seedlings in two contrasting habitats: patches of the dominant shrub (*Ziziphus lotus*), and open interspaces; and (2) reproductive output of plants naturally occurring in both habitats. The two species were significantly aggregated. Transplanted *Asparagus albus* seedlings had higher survival rates in patches than in the open. Plants produced more flowers, fruits, and showed a higher mass of seeds when living in aggregates than when isolated. The mechanisms responsible for this facilitative effect seem to be related to soil enrichment in patches. These results suggest that the spatial aggregation of species can be indicative of a positive interaction among them, directly affecting fitness of at least one of the species. Facilitation, by inducing variations in the reproductive performance may play a major role in the demography and dynamics of plant populations.

Keywords Facilitation · Species interactions · Plants · Reproduction · Spatial distribution pattern

Introduction

There is growing evidence that negative and positive interactions operate simultaneously in plant communities

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(Chapin et al. 1994; Callaway and Walker 1997; Holzapfel and Mahall 1999; Pugnaire and Luque 2001). Positive interactions, however, are increasingly proposed as ubiquitous forces driving community structure and function (Bertness and Callaway 1994; Callaway 1995; Stachowicz 2001; Callaway et al. 2002). There are now many examples of positive interactions among plants, ranging from nurse-plant effects, i.e. enhanced growth and survival of seedlings living under trees and shrubs (Egerton et al. 2000; Tewksbury and Lloyd 2001), to shrubs and trees enhancing growth of understorey herbaceous plants (Pugnaire et al. 1996a, 1996b; Holzapfel and Mahall 1999). Positive interactions occur in very different plant communities and climates, from desert (Went 1942; Tielbörger and Kadmon 1995) to arctic environments (Brooker and Callaghan 1998), and are often related to the spatial clumping of species, as plants tend to aggregate spatially under harsh environments (Schlesinger et al. 1990; Montaña 1992). This aggregation has frequently been considered evidence of a positive interaction between clumped species (Haase et al. 1997; Kikvidze and Nakhutsrishvili 1998; Eccles et al. 1999), although the link of spatial clumping and positive interactions has seldom been tested. There is, however, evidence that spatial distribution of species has a considerable effect on the growth and reproduction of interacting plants, hence on the number of species coexisting in the community (Stoll and Prati 2001).

Interaction with neighbouring plants can influence reproductive success. However, community studies have rarely examined the fitness component of facilitation (but see Shumway 2000; Tielbörger and Kadmon 2000). When analysing fitness it is important to examine its different components and to consider different life stages, because the several components of fitness provide different information on the ecological behaviour of the species (Howard and Goldberg 2001), and because the outcome of the interaction between species can shift with plant age (Pugnaire et al. 1996a; Rousset and Lepart 2000). Under this point of view, what is ultimately relevant for plant fitness is the balance between negative and positive

effects of neighbours (Brooker and Callaghan 1998; Rousset and Lepart 2000; Pugnaire and Luque 2001).

In an attempt to link spatial patterns and ecological interactions, we analysed the spatial distribution of two shrub species and assessed the consequences of their interaction for the smaller species in semiarid SE Spain. Reproductive success was measured at two different life stages, seedling survival and adult reproductive output, in order to assess the overall effect of facilitation on fitness. In arid ecosystems, where plants are often clumped in patches and cope with harsh conditions, facilitation seems to be a common process and any environmental amelioration caused by one plant may lead to an important positive response in a neighbour.

Two general hypothesis were tested using this two-tiered system: (1) the spatial aggregation of species can be indicative of underlying positive effects, and (2) positive interactions can have significant effects on fitness of the interacting species, increasing performance and reproductive output.

Materials and methods

Study area

The study site is a semiarid coastal dune-strip located in the Natural Park of Cabo de Gata-Níjar, Almería, Spain (36°50′N, 2°23′W). The climate is dry Mediterranean, characterized by low irregular annual rainfall (mean 204 mm), mild winter temperatures (mean winter minimum above 8°C), and hot summers (mean summer maximum of 30.3°C). Soil is sandy and shaped by semi-mobile dunes, fixed by vegetation over a glacis of quaternary origin and fossil beaches.

Vegetation occurs in clear, discrete patches, separated by low-cover ground. Patches are dominated by *Ziziphus lotus* (L.) Lam. (Rhamnaceae), a thorny shrub that forms large hemispherical canopies 1–3 m in height and congregates many other species of shrubs and herbs. The canopies are profusely ramified, with intricate branches. Each canopy of *Ziziphus lotus* (*Ziziphus* hereafter) covers approximately 10–20 m². Microclimatic conditions inside the canopy, including the accumulation of large amounts of drifting and organic matter, are very different from the surrounding matrix (Tirado 2003).

Asparagus albus L. (Liliaceae) was chosen as a target shrub because it is a common plant that grows in gaps in the area but most often associated with other shrubs, mainly *Ziziphus*, and is easy to differentiate as discrete individuals. *Asparagus albus* (*Asparagus* hereafter) is a spiny shrub up to 0.9 m tall, with several woody stems emerging from a cluster of fleshy storage tubers. The plants have deciduous cladodes that fall at the end of the growing season (May–June). Flowers are hermaphrodite and bloom abundantly at the end of the summer. The fruits ripen by fall (late September–October) and are dispersed by birds.

Spatial analysis

One 150 m ×150 m plot was selected and subdivided into 36 subplots 25 m ×25 m in November 1999. The coordinates of the estimated centre of every individual of *Ziziphus* and *Asparagus* taller than 10 cm were recorded to the nearest 5 cm. For *Ziziphus* canopies the maximum diameter and its perpendicular were measured in order to relate the spatial distribution of *Asparagus* to *Ziziphus* size. *Asparagus* individuals were divided into two size classes depending on their diameter (≤0.2 m or >0.2 m).

Spatial distribution patterns were analysed using Ripley's *K* function (Ripley 1976; Haase 1995), generally considered the best technique for bivariate point pattern analysis (Dale 1999). The *K*-function considers each plant as a central point of a circle of radius *t*, counting the number of points found within the circle. The weighting approach, used to correct for edge effects (Getis and Franklin 1987; modified by Haase 1995), yields unbiased results for distances up to half of the shortest side of the plot (Haase 1995). If the distribution of the points is Poisson random, the expected value of the cumulative function $K(t)$ equals πt^2, i.e. the area of a circle of radius *t*, which gives a linear plot of $\sqrt{K(t)}$ versus *t*. For an easier interpretation, the derived sample statistic $\sqrt{K[(t)/\pi]}-t$ is generally plotted as this expression has a zero expectation for any value of *t* when the pattern is Poisson random (Sharpe 1991).

The null hypothesis of spatial randomness was tested by randomly re-positioning all points in the plot and then analysing the generated plot as mentioned above. For statistical significance, we used the values at the limit of the 2.5% tails of 1,000 randomizations (mean±1.96 SD) for 95% confidence intervals. If the deviation of the sample statistic from zero expectation is significantly positive, the sampled points are assumed to be aggregated, while significant negative deviation suggests a regular (uniform) pattern (Diggle 1983). If the sample statistic remains within the bounds of the confidence interval at any given *t*, the null hypothesis of complete spatial randomness cannot be rejected. A plot of $\sqrt{K[(t)/\pi]}-t$ versus *t* reveals spatial patterns at various values of the neighbourhood distance *t*.

The null hypothesis of complete spatial randomness was tested for the two species, *Ziziphus* and *Asparagus*, with a modified procedure for analysis of bivariate distribution patterns, and statistical analysis of the data was performed using the SPPA program (Haase 2001).

Seedling transplant experiment

If the aggregation of *Asparagus* in *Ziziphus* patches is a consequence of a positive interaction between the two species, we should find higher survival, growth or fitness of *Asparagus* individuals living in *Ziziphus* patches than individuals living in the open. To test this hypothesis we transplanted *Asparagus* seedlings both in patches and in open spaces. Eighty seedlings of *Asparagus* were extracted in February 2000 from the field site, mainly from patches of *Ziziphus*. Seedlings were planted in pots containing 50% of soil from patches and 50% from the open, and taken to a common garden where they were watered as required. After 1 month each seedling was randomly planted either under the canopy of a *Ziziphus* individual (*n*=40) or in a gap (*n*=40). Patch and open sites were paired to minimize spatial heterogeneity. Plants were watered for 3 weeks following transplantation in the field to avoid drought shock since the season was extremely dry. After 9 months plants were sampled and survival values were compared by a chi-square test.

Fitness response to aggregation

The reproductive success of mature *Asparagus* shrubs was examined in the open and in neighbouring patches of *Ziziphus*. Because of the low number of *Asparagus* plants growing isolated, replicates were limited to six.

The number of stems on every plant was counted at the time of flowering (September 2000): two flowering stems were chosen at random and marked in order to follow their development. The total number of flowers per plant was estimated by counting the number of flowering stems per plant, the number of flowering nodes per selected stem, and the number of flowers per node in five random nodes, and by multiplying these values. At fruiting time (October) we estimated the total number of fruits per plant as we did for flowers. When fruits were ripe, we collected and weighed 10–15 fruits per plant (number of replicates limited by the low fruit production in the open), and then separated, counted, and weighed

the seeds. Comparisons of the reproductive output variables for plants inside and outside *Ziziphus* patches were made by non-parametric Mann-Whitney U tests, as variables were not normally distributed or normalized after transformation.

Results

Spatial analysis

Seventy-nine *Ziziphus* and 129 *Asparagus* individuals were recorded. The mean diameter of the *Ziziphus* patches was 12.5 m and the mean height 3.13 m. The spatial pattern of the two species showed a significant trend to aggregation (Fig. 1). There was a strong, statistically significant association between *Ziziphus* and *Asparagus* (Fig. 2), as individuals of *Asparagus* appeared more within *Ziziphus* patches than is gaps or associated with other shrub species, as shown by the Ripley's *K* statistic.

Seedling transplant experiment

Survival of *Asparagus* seedlings was very different depending on the location ($\chi^2=4.77$, $df=1$, $P<0.029$). Only 10% of seedlings planted in open habitats survived, while in patches 32.5% of the individuals continued to grow 9 months after planting.

Fitness response to aggregation

All measures of reproductive success were significantly higher for plants living in *Ziziphus* patches than for plants in the open (Table 1), except for average fruit mass, which did not differ ($Z=1.32$, $P=0.19$) (Fig. 3a). The total number of flowers, total number of fruits, and total seed mass per plant were approximately 85% higher for plants in patches than for plants in the open. Plants living in association exhibited a greater production of all reproductive units. Plants in patches produced more flowering nodes per stem and a higher number of flowers per node. At the population level, 88% of seeds were produced by plants in patches while only 12% were produced by those in the open (Fig. 3b, c). All fruits were one-seeded (except for four three-seeded berries from one plant), so the
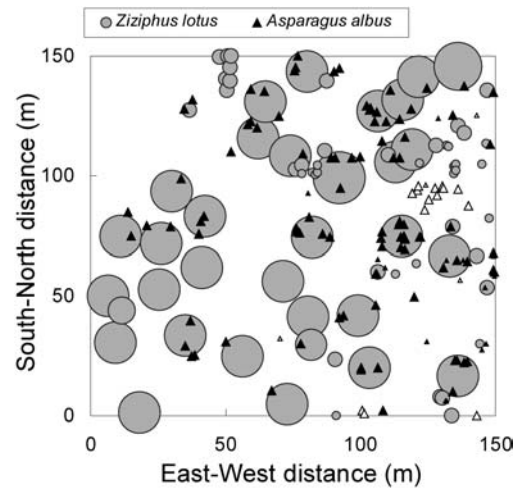
Fig. 1 Distribution map of *Ziziphus lotus* and *Asparagus albus* in a sand dune-strip on the Almería coast, SE Spain. Shrubs are drawn to scale according to three size classes ($\leq$1 m, 1–4 m, and >4 m) for *Z. lotus* and two ($\leq$0.2 m and >0.2 m) for *A. albus*. *Clear triangles* represent *Asparagus* plants with other shrub species
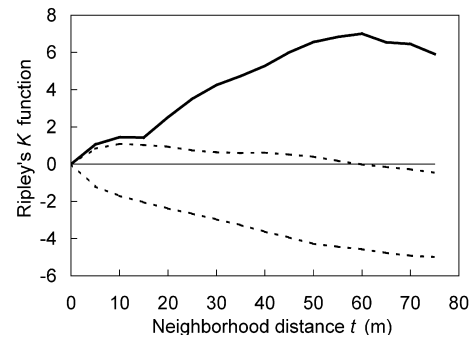

Fig. 2 Second-order spatial analysis of the distribution pattern of *A. albus* and *Z. lotus*. The plot of the derived statistic of Ripley's *K* function $[\sqrt{K(t)/\pi}-t]$ versus *t* reveals spatial patterns at increasing values of the neighbours distance *t*. Positive values indicate aggregation, while negative ones mean regularity. *Dotted lines* give 95% confidence intervals for complete spatial randomness from 1,000 randomizations

number of fruit equalled the number of seeds. The absolute measures of reproductive success expressed on a per individual basis showed a higher fecundity of plants in patches. In addition, a relative measure of reproductive

Table 1 Reproductive success variables of *Asparagus albus* plants living in *Ziziphus lotus* patches and in the open. Values are mean±SE, *n* =6. (Bold letters show statistically significant differences, $\alpha \leq 0.05$)

	Patches	Open	Z	P
Total stems	35.8±12.9	27.5±5.0	0.08	0.94
Percent flowering stems	37.6±4.7	23.8±5.1	1.68	0.09
Flowering nodes / stem	158.8±23.1	44.1±14.4	2.72	**0.006**
Flowers / node	10.8±0.6	6.1±0.4	2.88	**0.004**
Flowers / stem	1,725±279	291±108	2.72	**0.006**
Flowers / plant	20,250±6,193	3,505±2516	2.56	**0.01**
Fruiting nodes / stem	125.9±18.3	28.0±17.3	2.40	**0.01**
Fruits / node	4.0±0.3	1.4±0.4	2.88	**0.004**
Fruits / stem	505.3±77.9	54.2±35.3	2.88	**0.004**
Fruits / plant	5,813±1,834	826±740	2.56	**0.01**
Fruit set (%)	30.3±3.2	12.2±4.6	2.24	**0.02**
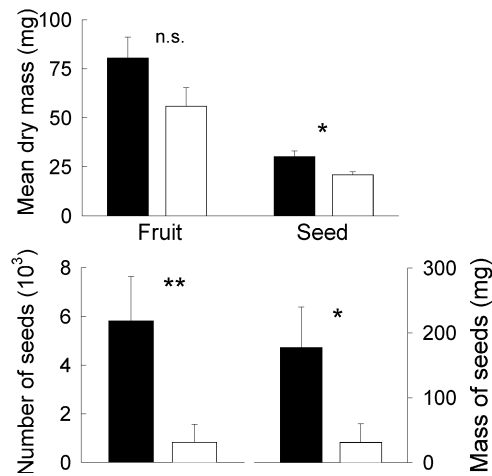
Fig. 3a–c Reproductive output of *A. albus* individuals living in patches (*solid bars*) and in the open (*clear bars*). **a** Average fruit and seed mass. **b** Total seed number per plant. **c** Total seed mass production per plant. Values are mean ±1 SE; $n=6$ for plants in patches and $n=4$ for plants in the open, since two plants did not produce mature fruit. Statistically significant differences between individuals in patches and in the open denoted by * for $\alpha=0.05$ (U Mann Whitney test) and by ** for $\alpha=0.01$

success, i.e. the proportion of flowers setting fruits (fruit set), was also higher for plants in patches. Hence, the plants in patches not only produced more flowers, but also a higher proportion of those developed into mature fruits. Associated plants also produced heavier seeds (Fig. 3a). The number of seeds, the average seed mass, and the total seed biomass produced by individual plants differed in both habitats (Fig. 3).

Discussion

The field data support our hypothesis that the spatial distribution pattern was a consequence of an interaction between the two species, with effects on plant fitness. *Asparagus* was associated significantly with *Ziziphus*, and plants living in patches or in the open differed widely in reproductive success. Seedling survival, plant fecundity, and reproductive mass were significantly higher for plants living in *Ziziphus* patches, suggesting that the spatial aggregation of the species can reflect an interaction that directly affects fitness.

The spatial aggregation of plants is well documented in arid and semi-arid environments, where vegetation is often arranged in a two-phase mosaic composed of high-plant cover patches in a low-cover matrix (Montaña 1992; Aguiar and Sala 1999). Some authors have argued the importance of this pattern in determining the nature of the interaction between species, indicating a positive interaction (Haase et al. 1997; Kikvidze and Nakhutsrishvili 1998; Eccles et al. 1999). Population dynamics and interaction of species can be influenced by the spatial structure (Czárán and Bartha 1992) although predictions of 'spatial theory' have not been subjected to much

empirical testing (Steinberg and Kareiva 1997). Thus, there is a relative lack of empirical evidence linking spatial aggregation of plants with interspecific facilitation. Our results showed how the clumping of one shrub species with another can dramatically change reproductive output.

Spatial heterogeneity of resources alone may influence the spatial pattern in the field. In arid and semi-arid ecosystems spatial heterogeneity has long been associated with the presence of shrubs (Went 1942; Pugnaire et al. 1996a, 1996b; Reynolds et al. 1999); however, this variation may be related to stochastic spatial heterogeneity. Since our plot is in a rather homogeneous glacis of erosion with no observable geological differences, we assume that the spatial heterogeneity of resources is most likely caused by the ability of *Ziziphus* to act as an 'ecosystem engineer' that modifies its surrounding environment. In fact, the spatial distribution of *Ziziphus* shrubs is random (Tirado 2003), suggesting that the observed effects are biological rather than caused by micro-environmental conditions.

When examining the intensity of the interaction between plants, more than a single fitness component or life stage should be analysed, because the relative importance of each fitness component is critical in understanding community structure (Howard and Goldberg 2001). In this study, the multiple responses to spatial aggregation shown by *Asparagus* suggested several levels of effects of one plant on another. Seedlings mainly survived when growing within the *Ziziphus* canopy, suggesting a nurse-plant effect in the early stages of *Asparagus*. Mature plants in patches produced a higher number of seeds and a higher reproductive biomass than plants in the open, evidencing an overall continued facilitative effect. Therefore, both the demography and population dynamics of *Asparagus* were strongly influenced by the positive interaction.

The increased reproductive output of *Asparagus* living in patches results from differences at three stages of reproduction. Plants in patches produced more flowers, set a higher proportion into fruit, and produced heavier seeds. Differences in flower and seed production are likely caused by limited maternal resources (Weiner 1988; Venable 1992). Besides, fruit set is constrained by both limited pollen supply (e.g. Herrera 1991; Burd 1994) and inadequate maternal resources (e.g. Stephenson 1981). If these factors vary spatially (i.e. in patches vs the open), they may be responsible for the differences found. Thus, the reproductive advantage of living in patches is the higher availability of resources that enables plants to increment reproductive output in a more favourable environment.

The consequences of intraspecific variation in reproductive output within plant populations can be relevant to population structure and dynamics (Wilson 1998; Herrera 2000). The *Asparagus* population is structured into two spatially separate habitats: *Ziziphus* canopies and open interspaces. *Asparagus* plants living in patches provided most of the seeds (88%) of the whole population. For this

	Patches	Open
Flowers	85	15
↓		
Fruits	25.5	1.8
↓		
Seedling survival	8.3 (97.6%)	0.2 (2.4%)
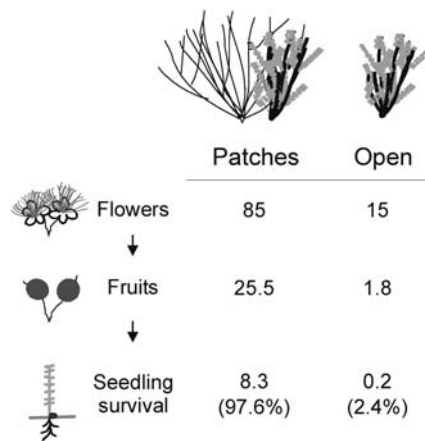
Fig. 4 Potential contribution of patches and open habitats to *A. albus* whole-population reproductive output, derived from the observed rates and values in each habitat

reason, patches possibly act as 'sources' and open sites as 'sinks' of seeds. Shmida and Ellner (1984) showed that seed input from neighbouring habitats can maintain 'sink' populations in annual desert communities that would otherwise be 'non-viable'. The potential reproductive contribution of each habitat to the whole *Asparagus* population was estimated by combining reproductive variables in patches and open habitats (Fig. 4). This estimation considered each habitat as a separate compartment, without exchange of propagules and with equal seed germination rate. The difference between patches and open sites increased throughout the reproduction process, providing a huge difference at the end between seedlings produced in the two habitats.

Larger seeds generally give rise to seedlings with better performance (Winn 1988; Dawson and Ehlenringer 1991; Chacon and Bustamante 2001). *Asparagus* plants in open habitats produced seeds with less endosperm storage, which potentially decreases seedling survival and growth. Thus, at the community level, the positive effect of *Ziziphus* on *Asparagus* can have important long-term consequences for the dynamics and stability of the population of this species. In desert plant communities, demographic responses of annual plants can be highly influenced by aggregation to shrub canopies, although the response is species-specific (Tielbörger and Kadmon 1995). Annual plants living under shrub canopies in a desert community achieved higher reproductive success than plants living in the open (Tielbörger and Kadmon 2000). Likewise, Shumway (2000) reported an increase in reproductive output in the number of flowers and seeds of two species of herbaceous perennials when living under a shrub canopy, while seedling survival was not affected by the location. Our results show that the positive influence of neighbours on plant fitness also includes perennial, woody plants in harsh conditions, and that the positive effect takes place at different life stages.

In summary, the spatial aggregation of these two shrub species revealed a strong facilitative effect of the larger species on the smaller species. This positive effect involved improving plant performance at different life stages and of different reproductive components, linking spatial distribution and plant performance and fitness. Patches where shrubs aggregate are a source of propagules with important effects on population dynamics. Thus, plant interactions, by triggering variations in plant reproductive performance, play a main role in vegetation dynamics.

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