Frugivorous birds mediate sex-biased facilitation in a dioecious nurse plant

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Abstract. Facilitation by dispersal occurs if the nurse plant acts as a focus which is actively selected by seed dispersers and enhances the fitness of the facilitated plant. Sex-biased facilitation may be produced if seed dispersers tend to concentrate the seeds under female, fruit-bearing plants of dioecious species more often than under conspecific males. *Juniperus sabina* is a dioecious shrub with a prostrate growth form from Mediterranean high mountains that modifies many microhabitat characteristics related to seedling establishment and survival. Soil water availability, maximum soil temperature in summer, organic matter and total nitrogen content, were different on open ground as compared with beneath *J. sabina* shrubs, irrespective of its sex. Other studied characteristics such as soil bulk density and soil compaction after rain did not differ between the microhabitats considered. Some species, such as *Juniperus communis*, *Pinus nigra*, *Helleborus foetidus* and *Euphorbia nicaeensis*, are spatially associated to *J. sabina* shrubs, strongly suggesting a facilitative role. The anemochorous *P. nigra* and myrmechorous *H. foetidus* and *E. nicaeensis* did not associate preferentially to any sex of *J. sabina*. Only *J. communis*, an endozoochorous species sharing the same bird dispersers as *J. sabina*, presented a female-biased spatial association with the nurse plant. Seed dispersal mediated by birds attracted by the fruit-rewarding females of *J. sabina* explains the sex-biased spatial pattern of *Juniperus communis*.

Keywords: *Juniperus communis*; *Juniperus sabina*; Mediterranean mountain; Plant-animal interaction; Seed dispersal.

Nomenclature: Mateo & Crespo (1998).

Abbreviation: PAR = Photosynthetically active radiation.

Introduction

In the seminal paper of Connell & Slatyer (1977) about mechanisms of succession, they proposed that facilitation occurs when "later (colonizing) species can become established and grow only after earlier ones have suitably modified the conditions (of the site)". Since then, a growing literature on facilitation has been published (see, e.g., Vetaas 1992; Wilson & Agnew 1992; Bertness & Callaway 1994; Callaway 1995, 1997; Callaway & Walker 1997; Holmgren et al. 1997; Brooker & Callaghan 1998; Callaway & Pugnaire 1999 and Olofsson et al. 1999 for a revision and discussion of the topic) and more operative definitions of facilitation are emerging, like that of Callaway & Pugnaire (1999): "Positive interactions, or facilitations, occur when one plant species enhances survival, growth, or fitness of another".

Although most of the studies focused on abiotic modifications of the habitat by the facilitator species, biotic mediated interactions have also been described. Callaway (1995, 1997) referred to the former as 'direct mechanisms' because the benefactor species modifies the physical habitat (light, soil, moisture etc.) which directly favours the colonization and growth of the facilitated species. Biotic mediated mechanisms were referred to as 'indirect mechanisms' because they involve other organisms (seed dispersers, pollinators, predators, fungi etc.) to mediate the interaction between species. Facilitation by dispersal may be produced if the benefactor species acts as (1) a non-specific trap for seeds transported by wind or water (Callaway 1995) or (2) a focus which is actively selected by dispersal agents, such as animals (Fuentes et al. 1984; Verdú & García-Fayos 1996). Nevertheless, for dispersal to be considered an indirect mechanism of facilitation, all or some of the components of the fitness of the facilitated plant must be enhanced beneath the benefactor species respective to plants dispersed elsewhere (Callaway 1995). This condition can be fulfilled when the benefactor species also provides a more favourable microhabitat to seed survival, germination, establishment and seedling

growth, survival or reproduction of the facilitated plant.

In mediterranean ecosystems, bird dispersers have the potential to spatially concentrate the seeds of different species because they feed on their fruits and regurgitate or defecate seeds together in selected places (Herrera 1984; Debussche et al. 1985; Izhaki et al. 1991; Debussche & Lepart 1992; Herrera et al. 1994; Alcántara et al. 2000). In addition, if the species attracting birds are able to ameliorate the microhabitat for plant establishment, then direct facilitation can also occur (Verdú & García-Fayos 1996, 1998). A few studies on bird-dispersed plants have shown that seed dispersers may produce a sex-biased dispersal because they tend to concentrate the seeds under female plants of dioecious species more often than under conspecific males (Herrera 1988; Herrera et al. 1994). In these species, only females produce fruits and may act as a focus which is actively selected by frugivorous birds. However, it is unknown to what extent female nurse plants ameliorate the microhabitat for dispersed seeds to germinate and establish differently than males. Because the spatial patterns of seed dispersal may be unrelated to the final pattern of seedling establishment (Jordano & Herrera 1995), sex-biased seed dispersal may not be necessarily translated into a sex-biased facilitation. In mediterranean high mountains, recruitment may be limited by low winter temperatures, water stress and herbivory (Arista 1994; García 1998; García et al. 1999, 2000). In these habitats, the dominant shrub *Juniperus sabina* densely covers the ground and may reduce moisture loss and herbivory, facilitating the establishment of other species. Birds of the genus *Turdus* disperse *J. sabina* seeds and also those of *J. communis* (Jordano 1993), a species that may potentially benefit from the microhabitat modification exerted by *J. sabina*. This supposed indirect facilitation process may be sex-biased because *J. sabina* is a dioecious species and fruiting females are expected to attract more birds than males. Then, a higher probability for *J. communis* seeds to be dispersed beneath *J. sabina* females may occur. In contrast, species with dispersal mechanisms other than ornithochory can also be facilitated by *J. sabina*, but they are not expected to show sex-biased associations. Thus, more precisely, we hypothesize that (1) conditions relative to establishment, growth and survival of plants are more favourable beneath *J. sabina* individuals than on the open ground, (2) a spatial association between *J. sabina* and other species, irrespective of their dispersal mechanisms, may exist and (3) only *J. communis* shows a greater rate of spatial association to females of *J. sabina* than to males.

Natural history of the system

This study was conducted in El Verdinal, a site near Puebla de San Miguel (Valencia, East Spain) (40º1' N, 1º12' W) at 1640 m a.s.l. Sampling was carried out in a 5-ha stand on a southwest oriented slope with 10º inclination. Soils are very shallow, less than 30 cm, but cracks in the limestone permit roots to go deeper. El Verdinal is part of an extensive karst system on massive calcareous limestones in the Javalambre mountains. In these mountains, *Juniperus sabina*, *J. communis*, *J. thurifera* and pines: *Pinus sylvestris* and *P. nigra* ssp. *salzmannii*, are the dominant species in open woodlands (Costa 1986; Peinado & Rivas-Martínez 1987). The discontinuous herb and subshrub layer is mainly composed of *Helleborus foetidus*, *Euphorbia nicaeensis*, *Helianthemum canum*, *Thymus godayanus*, *Koeleria vallesiana* and *Festuca hystrix*. For centuries, the human exploitation of these areas has been mainly for timber (*Pinus* and *J. thurifera*), fuel (*Pinus* and *J. communis*), extensive livestock (sheep and goats) and agriculture. The study area has been used for extensive livestock grazing for a long time, maintaining a steady grazing pressure (0.3 sheep.ha^{-1}) for at least the two last centuries. Narrow valleys were tilled for rye and barley in the last century until land abandonment in 1960 (Rodrigo 1999). As a result of this traditional use, great extensions of land remain vegetated almost exclusively by scattered individuals of *J. sabina* producing a characteristic spotted landscape, relegating the other dominant *Pinus* spp. and *J. communis* to marginal areas. In the last decades, human desertion as a consequence of social and economic changes allowed a reversion of the process of deforestation (Lasanta 1996).

The climate is mediterranean, with harsh winters (January mean temperature 2.5 ºC) and a duration of the freezing period of more than 120 day.yr^{-1} and warm summers (July mean temperature 21 ºC). Mean annual precipitation is 600 mm and although there is a summer drought, violent and irregular storms are frequent during this period, resulting in more than 120 mm of annual summer precipitation (Pérez-Cueva 1994).

The studied *Juniperus* species differ in growth form habit and leaf type. *J. sabina* has cupressus-like leaves and a prostrate and creeping growth form developed in a centrifugous pattern, reaching diameters of up to 20 m. *J. communis* ssp. *hemisphaerica* is a semi-erect shrub up to 2.5 m high with aciculate leaves. Like many species of the genus, these are both dioecious. In the study area, cones (fruits) of *J. communis* are slightly smaller than those of *J. sabina* (6.45 ± 0.07 and 6.70 ± 0.10 mm diameter, respectively; $t = 2.05$; $df = 112$; $p < 0.05$), but they have more seeds per fruit (2.69 ± 0.02 vs 2.28 ± 0.02; $n = 1650$; $z = -13.4$; $p < 0.001$; Mann-Whitney test). Seeds of both species could be identified by the following characters:

J. communis has ellipsoidal, dim seeds with grooves and resin bags in all the seed; *J. sabina* has pyramidal, shining seeds with grooves only in the lower part of the seed and without resin bags. Fruits from both species ripen at the same time and are dispersed almost exclusively by birds of the genus *Turdus*, mainly *T. torquatus* and *T. viscivorus* (M, Verdú & P. García-Fayos, pers. obs.; Jordano 1993). The non-endozoochorous species considered in this study to contrast the spatial association pattern of *J. sabina* with the endozoochorous *J. communis* were *Helleborus foetidus* (*Ranunculaceae*), *Euphorbia nicaeensis* (*Euphorbiaceae*); *Pinus nigra* (*Pinaceae*). *H. foetidus* and *E. nicaeensis* are perennial herbs dispersed by ants (Molinier & Müller 1938) and *P. nigra* is an anemochorous tree. These species were selected because they represented different dispersal systems and were very abundant in the study area.

Material and Methods

Seed dispersal

To prove that *Turdus* birds were able to disperse the seeds from both *J. sabina* and *J. communis* simultaneously we collected 28 individual faeces of *Turdus* spp. and additional spare dung defecated in an adjacent fountain during November 2000. The number of seeds of both *Juniperus* species were counted and the volume fraction of seeds from other plant species and animals in the diet of the birds were estimated. The spatial pattern of *J. communis* seed rain was studied by sampling the seed bank in 60 plots placed randomly in three microhabitats as follows: 20 plots on open ground, 20 plots beneath *J. sabina* females and 20 plots beneath *J. sabina* males. Within each plot soil samples were collected in two 25 cm × 25 cm × 5 cm subplots that were at least 1 m apart. Soil samples were sieved at 1 mm and inspected for the presence of *J. communis* seeds.

Seed predation

On 01.12.2000, 22 Petri dishes each containing five *J. communis* seeds extracted from faeces were randomly placed in the same three microhabitats. Three dishes on the open ground and one beneath a male shrub disappeared and, therefore, the final number of dishes was 62. Two visits were made on 15.12 and 15.02 and because the results were significantly correlated (Spearman $\rho = 0.61$; $n = 62$; $p < 0.0001$) only results of the last visit will be shown. The number of seeds eaten from each Petri dish was analyzed by means of a generalized linear model following a Poisson distribution. Microhabitat was considered as a categorical factor. Data fit a Poisson distribution as the Kolmogorov-Smirnov test for Poisson distribution reveals ($z = 0.79$; $n = 62$; $p \gg 0.05$) and, because the variance increases with the mean. The dispersion parameter was calculated and included in the model. This model was run in the R 1.5.1 package (Ihaka & Gentleman 1996).

Microhabitat characteristics

The microhabitat characteristics measured beneath *J. sabina* and on the open ground were those related to seedling performance. They were photosynthetically active radiation (PAR), water availability in soil (soil moisture curves), soil compaction and bulk density (related to seedling root penetration) and nutrient content of soil (organic matter, nitrogen and phosphorus).

Comparative measures of microhabitat characteristics, except for maximum temperatures, were made in spring (11.05.1999) because this is the germination and seedling establishment season for *J. communis* on Mediterranean high mountains (García 1998). Because high temperatures could limit seedling survival during summer drought, they were recorded in summer (July 1999).

Light (PAR) arriving at the ground was measured at midday with a 1-cm diameter quantum sensor (Skye Instruments, Llandrindod-Wells, UK) beneath ten males, beneath ten females and on ten open ground points randomly selected in the study area. Each replicate consisted of three measures from which mean values were calculated. In the case of *J. sabina* plants, the three measures were: (1) at the centre of the shrub, (2) oriented towards the south and (3) oriented towards the north. In the case of the open ground, the three measures were taken at adjacent points, 1 m apart.

Daily maximum temperatures of the ground were obtained from temperature measures recorded hourly from 01.07-22.07.1999 with six thermocouple wires connected to a datalogger (Unidata, Willetton, AU). Because of limitations in the number of sensors, only two replicates per microhabitat (*J. sabina* males, females and open ground) could be taken. The same six locations were measured during the whole period. These replicates could not be randomly selected because all the measure points necessarily needed to be close to the datalogger. For these reasons, the statistical comparisons should be taken with caution.

Soil compaction was measured eight days after a 20-mm rainfall event with a hand penetrometer with a conic head which ranged from 5 to 400 N cm^{-2} (Eijkelkamp type IB, Giesbeek, NL) beneath ten males, beneath ten females and on ten open ground points randomly selected in the study area. Each replicate consisted of a mean of five measures. In the case of *J. sabina* plants, the measures were taken at the centre of the shrub and on

the four cardinal points. In the case of the open ground, the five measures were taken at adjacent points 1 m apart. The measure was discarded when the penetrometer made contact with a stone.

Soil bulk density was calculated as the dry weight of the soil contained in 5.35 cm × 6 cm cylindrical cores taken beneath six female and six male *J. sabina* shrubs and six points on the open ground randomly selected in the study area.

Soil moisture curves, organic matter, total N and soluble P were estimated from soil samples taken at the surface (to a depth of 5 cm) beneath ten female, ten male *J. sabina* shrubs and ten points on the open ground randomly selected in the study area. Soil moisture curves were determined by fitting the volumetric moisture content of soil samples at pF = – 0.02MPa, –0.08MPa, –0.5MPa, -1MPa and –1.5 MPa based on the methods proposed by Klute (1986). Organic matter, total N and soluble P were determined by the Walkley, Kjeldahl and Olsen methods respectively (Page 1982).

Orthogonal contrasts were constructed when the one-way ANOVA detected significant differences in microhabitat characteristic across open ground, males and females of *J. sabina*. Because our *a priori* hypothesis was that mean values of males and females are similar but differ from those of open ground, the orthogonal contrasts tested differences between (1) male vs female means and (2) the pooled mean of males and females vs the open ground mean. If the first contrast revealed sex-related differences, post-hoc multiple comparisons were performed with Tukey tests because an *a priori* hypothesis did not exist under this situation.

Normality and homogeneity of variances was checked and variables were transformed as needed (e.g. light was log-transformed). When normality or homoscedasticity could not be achieved by means of transformations, as in the case of soil compaction, a non-parametric test (Kruskall-Wallis) was used. If the same sampling unit received repeated measures, as in temperature (repetitions were the daily mean temperatures of 21 days in July) and soil moisture curves (repetition was the moisture contents of five pF points in the curve), analyses were performed by means of repeated measures ANOVA and the same *a priori* contrasts explained above were constructed. All the statistical tests were run in SPSS 9.0. Means and standard errors are presented throughout the text.

Spatial association patterns

The percentage of *J. sabina* canopy cover vs open ground was calculated by measuring the proportion of soil and *J. sabina* shrubs in 36 parallel 30-m linear transects 10 m apart.

To study the association between *J. sabina* and other species we recorded the number of *J. communis*, *P. nigra*, *H. foetidus* and *E. nicaeensis* individuals associated to (growing beneath) *J. sabina* shrubs and on the open ground. The existence of spatial association between *J. sabina* and each species was tested by comparing the observed (% individuals associated to *J. sabina*) against the expected (% *J. sabina* cover) frequencies.

Sex ratio of *J. sabina* did not differ from 1:1 (79 females: 66 males; $\chi^2 = 1.17$; $p = 0.3$). Size of *J. sabina* shrubs, calculated assuming an ellipsoidal shape and measuring two perpendicular diameters, did not differ between sexes (37.4 ± 3.2 m^2 and 35.1 ± 3.1 m^2 for females and males respectively; $t = 0.51$; $df = 143$; $p = 0.6$). The existence of a sex-biased spatial association between *J. sabina* and other species was measured by recording the number of female and male *J. sabina* shrubs with or without the study species. The presence of each species was recorded until the sample size was at least 100 *J. sabina* shrubs. Data were analysed by means of a 2×2 contingency table under the null hypothesis that the likelihood of a *J. sabina* shrub acting as a nurse plant is not dependent on its sex.

In the cases of the long-lived species *J. communis* and *P. nigra*, we excluded the oldest individuals from the analysis (79 and 20, respectively) to avoid the possibility that spatial association of these species with *J. sabina* was not caused by facilitation but by differential human exploitation (i.e. differential logging between associated and non-associated trees due to the higher accessibility of the latter). Oldest individuals of *J. communis* were considered to be those with a crown diameter > 2 m. This ensures that only seedlings, juvenile and the lowest reproductive adults are included in the analysis (Marion & Houle 1996). For *P. nigra*, only non-reproductive individuals were considered. The exclusion of the oldest individuals did not affect the results.

Results

Seed dispersal

J. sabina and *J. communis* fruits accounted for more than 99% of the volume fraction in the faecal material. The rest of the diet composed of worms and snails. Seeds of the two *Juniperus* species occurred together in 36% of the faeces, indicating that the same bird may disperse the two species simultaneously. These faeces contained 1.6 ± 0.3 *J. sabina* seeds and 4.8 ± 0.8 *J. communis* seeds. In 7% of the faeces, only seeds from *J. sabina* were found, with a mean of 3.0 ± 1.03 seeds. In 57% of the faeces, only seeds from *J. communis* were

Table 1. Microhabitat characteristics in the open ground, beneath female shrubs and beneath male shrubs of *Juniperus sabina*. Sample sizes were $n = 10$ for all cells except Bulk density where $n = 6$. Different letters in the same line show significant differences at $p < 0.05$.

	Male	Female	Open ground	Statistical test	Significance
PAR (log-transformed) ($\mu mol.m^{-2}.sec^{-1}$)	2.62 ± 0.11^a	2.53 ± 0.04^a	$3.23 \pm 6E\text{-}04^b$	$F_{2,28} = 27.7$	$p < 0.001$
Bulk density ($g.cm^{-3}$)	1.23 ± 0.13^a	0.88 ± 0.18^a	0.99 ± 0.06^a	$F_{2,17} = 1.45$	$p = 0.24$
Compaction ($Nw.cm^{-2}$)	0.08 ± 0.04^a	0.09 ± 0.03^a	0.08 ± 0.04^a	$\chi^2_2 = 0.39$	$p = 0.82$
Organic matter ($mg.g^{-1}$)	230.4 ± 16.2^a	260.3 ± 15.5^a	145.5 ± 18.5^b	$F_{2,29} = 12.5$	$p < 0.001$
Nitrogen content ($mg.g^{-1}$)	10.6 ± 0.6^a	12.5 ± 0.7^a	8.1 ± 1.0^b	$F_{2,29} = 6.4$	$p = 0.005$
Phosphorus content ($mg\text{-}P_2O_5.g^{-1}$)	0.026 ± 0.003^a	0.044 ± 0.006^b	0.022 ± 0.005^a	$F_{2,29} = 5.9$	$p = 0.008$

found, with a mean of 7.2 ± 0.8 seeds.

Birds dispersed the seeds of *J. communis* non-randomly because all the seeds were found beneath *J. sabina* shrubs, which represented only 25% of cover, whereas no seeds were found on the open ground. Moreover, birds concentrated their activity on *J. sabina* females: 75% of the sampled female shrubs (15 of 20) contained *J. communis* seeds against only 25% of males (5 of 20) ($\chi^2 = 10.0$; $df = 1$; $p < 0.005$).

Seed predation

A total of 45% of seeds placed experimentally in the three microhabitats were eaten. The mean number of eaten seeds per Petri dish was 2.2 ± 0.3 beneath males, 1.6 ± 0.3 beneath females and 3.1 ± 0.7 on the open ground, but these differences were not statistically significant ($p > 0.05$ for all the comparisons between categories in the Poisson regression).

Microhabitat characteristics

Soil properties related to seedling root penetration (soil compaction and bulk density) did not differ beneath *J. sabina* males, females or open ground after eight days of a spring rain (20 mm) (Table 1).

Mean values of soil moisture content at the extreme pressure points of the curve (–1.5 and –0.02 MPa) ranged from 35-59%, 39-63% and 22-46% for soil beneath males, females and on open ground respectively. The repeated measures ANOVA showed that the soil beneath males or females of *J. sabina* shrubs contained more water than that of the open ground (repeated measures ANOVA contrast for comparing male-female means was 2.66 ± 2.75; $p = 0.34$ and the ANOVA contrast for comparing male-female pooled means vs open ground mean was 12.44 ± 2.75; $p < 0.001$). These differences were consistent along all the pressure points of the curves because the interaction term of the repeated measures ANOVA was not significant.

Photosynthetic active radiation (PAR) did not differ beneath the canopy of male and female *J. sabina* shrubs.

Obviously, PAR on the open ground was significantly higher than beneath *J. sabina* shrubs (Table 1).

Maximum daily temperatures on the ground in summer (Fig. 1) were similar in male and female shrubs (repeated measures ANOVA contrast for comparing male-female means was 0.98 ± 1.12; $p = 0.44$). These temperatures were lower (around 9.3 ºC in average) than maximum temperatures on the open ground (repeated measures ANOVA contrast for comparing male-female pooled means vs open ground mean was -7.62 ± 1.12; $p = 0.006$). This difference was consistent throughout the study period as the non-significant interaction term of the repeated measures ANOVA indicates.

Organic matter and total nitrogen values were similar beneath male and female shrubs of *J. sabina* and these values were higher than those on the open ground (Table 1). Surprisingly, soluble phosphorus significantly differed between sexes, with a nearly two-fold higher concentration beneath females than beneath males of *J. sabina* shrubs (Table 1).
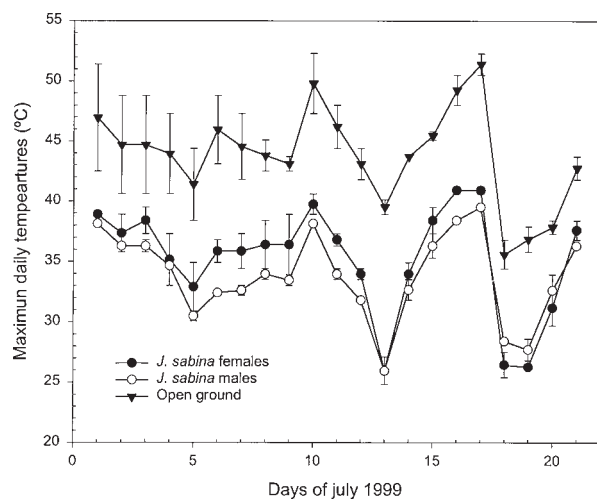

Fig. 1. Maximum daily temperatures in July 1999 beneath *J. sabina* female and male shrubs and on open ground.

Table 2. Number of individuals of each sex of *J. sabina* shrubs associated or non-associated to the study species.

	J. sabina with *J. communis*	*J. sabina* without *J. communis*	*J. sabina* with *P. nigra*	*J. sabina* without *P. nigra*	*J. sabina* with *H. foetidus*	*J. sabina* without *H. foetidus*	*J. sabina* with *E. nicaeensis*	*J. sabina* without *E. nicaeensis*
J. sabina male	16	49	38	46	24	29	37	16
J. sabina female	32	44	36	44	23	27	32	18
	$\chi^2 = 4.773$; $p = 0.029$		$\chi^2 = 0.001$; $p = 0.976$		$\chi^2 = 0.005$; $p = 0.942$		$\chi^2 = 0.393$; $p = 0.531$	

Spatial association patterns

The percentage of *J. sabina* canopy cover in the study area was only 25%. By contrast, 86.4% (70 of 81) of *J. communis* individuals were associated with *J. sabina* shrubs. *J. communis* individuals had a similar sex-biased association to females of *J. sabina* as seed shadow, because 42% of the sampled females contained *J. communis* adult plants whereas only 25% of males did (Table 2).

Other non-endozoochorous species were also associated to *J. sabina* shrubs more frequently than expected. Individuals associated to *J. sabina* shrubs were 47.8% of the total number of individuals of the anemochorous *Pinus nigra* ($n = 90$); 99% of the myrmechorous *Helleborus foetidus* ($n = 299$) and 87% of myrmechorous *Euphorbia nicaeensis* ($n = 388$) (all χ^2-square tests revealed $p < 0.001$). However, none of these species presented a female-biased spatial association with the nurse plant as did the endozoochorous *J. communis* (Table 2).

Discussion

J. sabina shrubs modified some of the microhabitat characteristics under their canopy. Thus, soil water availability, maximum soil temperature in summer, organic matter and total nitrogen content were different beneath *J. sabina* shrubs and open ground, but soil bulk density and compaction after rain were not.

The high organic matter and nitrogen enrichment in the soil may be a consequence of litter deposition and decomposition beneath *J. sabina* shrubs. An increase in nutrient content beneath nurse plants may favour seedling growth (Walker & Chapin 1986; Pugnaire et al. 1996), but see Grubb et al. (1996) who found little or no effect of nutrient supply on *J. communis* seedling growth and survival.

The shade provided by the canopy of the nurse shrubs may protect seedlings from desiccation by decreasing soil temperatures during summer and enhancing the soil water balance (Callaway 1995). The establishment of *J. communis* under mediterranean conditions has been reported to be strongly limited by summer stress (García 1998; García et al. 1999) and, therefore, the protection provided by the canopy of *J. sabina* may be an important factor in the population dynamics of *J. communis* by enhancing seedling survival. Shade may also reduce energy for photosynthesis in facilitated plants (Callaway 1995), but this negative effect on *J. communis* must be short-lived because seedlings of *J. communis* may quickly surpass the prostrate canopy of *J. sabina*. The favourable micro-environmental characteristics for seedling establishment beneath the canopy of *J. sabina* relative to the open ground may facilitate *J. communis* and the spatial association reported here supports this hypothesis. The other studied species had a strong spatial association to *J. sabina*; this indicates that they are able to benefit from the same modified microhabitat characteristics beneath the canopy of *J. sabina*.

Protection from predators and herbivores may also act as a facilitative mechanism. However, postdispersal seed predation rates of *J. communis* were similar beneath *J. sabina* shrubs and on the open ground. Although it was not quantified here, *J. sabina* shrubs could play an additional facilitative role by protecting seedlings from trampling and grazing by herbivores (Fitter & Jennings 1975; Clifton et al. 1997; García et al. 2000).

Spatial associations between species may result from confounding effects of shared physical microhabitat requirements (Callaway 1995). Because *J. sabina* and associated species may have common microhabitat requirements, the spatial association may be only a spatial coincidence. However, we discard this possibility for two reasons: (1) physicochemical soil properties are strongly homogeneous at the regional level (Rubio et al. 1997), suggesting that the soils of the study area cannot be considered as a mosaic of microhabitats that permit differential colonization by several species sharing the same requirements and (2) the individuals of the species associated to *J. sabina* established after – and not before – *J. sabina*. The latter is true because they were short-lived (*H. foetidus* and *E. nicaeensis*) or if long-lived (*J. communis* and *P. nigra*), only pre-reproductive or the lowest reproductive individuals were included in the analysis (see Methods). This supports the hypothesis that these species established when the microhabitat had

already been changed by *J. sabina*. Additionally, *J. sabina* only establishes in sunny microhabitats and therefore it is not likely to establish beneath other plants (M. Verdú & P. García-Fayos pers. obs.).

In our study area, *J. communis* also establishes without the facilitative effects of *J. sabina* when environmental conditions improve. In cultivated valleys abandoned ca. 35 years ago, with deeper and wetter soils, the density of *J. communis* was 3.5 times greater than on slopes, and it is not associated with *J. sabina*. This variation in the intensity of the facilitative interactions fits well with the predictions of the model proposed by Bertness & Callaway (1994) and has also been described for other *Juniperus* species (Chambers et al. 1999; Chambers 2001).

Our data show that the spatial distribution patterns of *J. communis* seeds and adults are biased with regard to the sex of its nurse plant. Avian seed dispersers may produce this bias because they preferentially fly to fruit-bearing shrubs (females) and a single bird can disperse seeds from both plants simultaneously. Other studies have also found a female-bias in the fate of the seeds dispersed by birds, e.g. Herrera (1988) and Herrera et al. (1994) who describe that females of the dioecious plant *Pistacia lentiscus* received more seeds of *Osyris quadripartita* and *Phillyrea latifolia* than conspecific males. An additional line of evidence about the role of birds in the sex-biased distribution pattern is that none of the other studied – anemochorous and myrmechorous – species showed this bias. The spatial concordance between the sex-biased distribution of *J. communis* seeds and adults suggests that the female-biased seed shadow generated by birds was not qualitatively modified by post-dispersal processes. Post-dispersal events such as seed predation or microhabitat characteristics related to seed germination and seedling growth beneath nurse plants did not differ between sexes, except soluble phosphorus in the soil. The higher phosphorus concentration found beneath *J. sabina* females than beneath males may be caused by the differential accumulation of bird faeces and abscised fruits. The differential P-concentration may reinforce the female-biased spatial pattern of seed rain generated by frugivores if seedling survival is limited by this element.

In conclusion, *J. sabina* plays an important facilitative role on the dynamics of colonization by other species by the amelioration of microhabitat characteristics. Additionally, females of *J. sabina* have an indirect facilitative role by concentrating seeds of endozoochorous species, such as *J. communis*. Because this can shape the dynamics of plant communities we propose taking into account not only the direct facilitative effects of some plants but also their sexual consequences for the restoration and management of the communities.

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