

POLLINATION CONTEXT EFFECTS IN THE HIGH-MOUNTAIN DIMORPHIC *ARMERIA CAESPITOSA* (PLUMBAGINACEAE): NEIGHBORHOOD IS SOMETHING MORE THAN DENSITY¹

RAÚL GARCÍA-CAMACHO,² MARCOS MÉNDEZ, AND ADRIÁN ESCUDERO

Área de Biodiversidad & Conservación, Universidad Rey Juan Carlos- E.S.C.E.T., Tulipán s/n. 28933 Móstoles, Spain

Frequency-dependent processes are relevant for flowering plant reproduction, especially for species with disassortative mating. In an individual-based study, we tested not only the effects of local density on reproductive success at small spatial scales, but also those of neighborhood quality. To test the neighborhood effects on the reproduction of *Armeria caespitosa*, a dimorphic Mediterranean high-mountain endemic, we introduce a novel pollination context (PC) index that considered the distance, floral display, and floral morph of neighbors at small scales (within 2 m from the focal plant), studying rock and pasture populations at both edges of the species altitudinal distribution. Reproductive success depended significantly on PC only at the low populations, suggesting that the PC effects are population-dependent and supporting the hypothesis that the neighborhood quality influences the reproductive success of *A. caespitosa* at least in stressful conditions. Moreover, fruit set was morph-dependent in the high-pasture population. The specific role of the spatial structure of compatible vs. incompatible morphs at small scales of the dimorphic self-incompatibility system in *Armeria* deserves further attention. Parameters other than plant density are useful for the study of small-scale density-dependent processes that affect pollination and other reproductive components, especially if they integrate neighborhood quality information at adequate spatial scales.

Key words: *Armeria caespitosa*; density dependence; frequency dependence; Mediterranean mountains; narrow endemism; plant reproduction; Plumbaginaceae; self-incompatible system.

Insect-pollinated plants, whose reproduction is constrained by the availability of conspecific pollen (Burd, 1994; Larson and Barrett, 2000; Ashman et al., 2004; Knight et al., 2005; García-Camacho and Totland, 2009), are especially sensitive to variations in population attributes concerning the spatial distribution of individuals. For instance, plant isolation from outcross pollen (Groom, 1998; Duncan et al., 2004), habitat fragmentation (Aizen and Feisinger, 1994), and plant density at different scales (Roll et al., 1997; Bosch and Waser, 2001; Colling et al., 2004; Spigler and Chang, 2008) limit plant reproduction. In this context, Allee effects are common among self-incompatible species (Luděc et al., 2006). Pollination and fertilization success decrease in small or sparse populations that, being less attractive to pollinators, receive fewer visits (Kunin, 1997; Mustajärvi et al., 2001; Feldman, 2006; Aizen and Harder, 2007; Makino et al., 2007), resulting in lower seed sets (Ågren, 1996; Kunin, 1997; Bosch and Waser, 1999; Duncan et al., 2004; Ishihama et al., 2006; Steven and Waller, 2007).

Species with disassortative mating between members of two groups, for which reproduction of one group depends on the availability of pollen from the other, are particularly sensitive to density- and frequency-dependent processes (Méndez and Díaz, 2001; Stehlik et al., 2006). For these species, the relative group abundance (Brys et al., 2007, 2008), the opposite morph density at a scale of a few meters (Widén and Widén, 1990;

Ishihama et al., 2006), and the spatial distribution of potential mates in local neighborhoods (Stehlik et al., 2006) are additional factors that determine reproductive success. Conventionally, density (individuals per unit area) has been used in population-based studies as a mean value assigned to each population. Although population density may be useful for estimating individual reproductive success (Luzuriaga et al., 2006), it ignores any differences in densities between individual plant neighbors within the same population (Spigler and Chang, 2008) and other characteristics of the small-scale spatial distribution of compatible mates within the population (Stehlik et al., 2006). For a single individual, different density values may be obtained depending on the scale considered (Kunin, 1997; Gunton and Kunin, 2007, 2009), and contrasting ecological processes may operate at such spatial scales, so it is necessary to take into account the scale at which each process should be studied (Gunton and Kunin, 2007; Spigler and Chang, 2008; Gunton and Kunin, 2009).

We present an individual-based study for testing not only the effects on reproductive success of local neighborhood density, but also the quality of those neighborhoods in terms of their potential pollen type and production (Le Cadre et al., 2008), the spatial arrangement of pollen donors at two within-population spatial scales, as well as the focal plant floral display size. For this purpose, we calculated an original index that accounted for these features of local neighborhood. We called it pollination context index (hereafter PC), referring to a term previously coined to integrate factors that potentially affect plant pollination and reproduction but on which natural selection cannot act (Méndez and Díaz, 2001). Most previous papers studying density and frequency effects on reproductive success have only focused on single factors (e.g., interplant distance, plant density, frequency of compatible morphs), or relatively simple combinations of those factors (Le Cadre et al., 2008). Our PC index, however, integrates such factors from a more realistic ecological perspective, integrating the abundance of flowers at

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² Author for correspondence (e-mail: raul.garcia@urjc.es)

all distances from the target plant (see Méndez and Díaz, 2001; Stehlik et al., 2006).

In this context, *Armeria caespitosa* (Gómez Ortega) Boiss. in DC. (Plumbaginaceae) is an excellent model to test how variation in pollination context may affect fitness. This species is a high-mountain plant, narrow endemic to the Iberian Sistema Central (Nieto Feliner, 1990). It grows in two contrasting microhabitats: in cracks and ledges on granitic outcrops and in high-altitude fescue fellfields. As most species of its genus, it is a sexually dimorphic, self-incompatible plant (Baker, 1966). High-mountain plant population densities and their pollination contexts may vary along elevational gradients (Gómez, 1993) and among microhabitats (Hansen and Totland, 2006). The pollinator assemblages could also vary along the elevational gradient.

More specifically, from a small-scale, individual-focused perspective, we hypothesized that reproductive success might be morph-dependent because both morphs could have different reproductive success. Besides, we hypothesized that female reproductive success in *A. caespitosa* would depend on its conspecific neighborhood quality. We differentiated the neighborhood into compatible and incompatible neighbors and calculated separate indices for them. Whereas we expected the compatible neighborhood to favor reproductive success of focal plants, the incompatible neighborhood could have detrimental effects by interfering with intermorph pollination (Nishihiro and Washitani, 1998). Finally, we considered that the effect of PC might vary between populations, so we evaluated the effect of PC on populations exposed to contrasting environments along the narrow distribution range of *A. caespitosa*, thus summarizing the entire environmental heterogeneity faced by this high mountain specialist.

MATERIALS AND METHODS

Plant natural history—*Armeria caespitosa* (Gómez Ortega) Boiss. in DC. is a high-mountain dwarf chamaephytic cushion plant, endemic to the Iberian Sistema Central. It occurs at Ayllón, Guadarrama, and East Gredos ranges, at altitudes from 1500 to 2430 m a.s.l. To the west of East Gredos massif, the species forms hybrids with another orophillous endemic, *A. bigerrensis* subsp. *bigerrensis* (Nieto Feliner, 1990).

Armeria caespitosa occurs in two interspersed but contrasting microhabitats: in crevasses and ledges of granite and gneiss outcrops (hereafter, rock microhabitat) and in dry cryophilic *Festuca curvifolia* pastures (hereafter, pasture) where it is often a dominant species. Its pink flowers are grouped in short-scaped flowerheads with 19 ± 8 flowers per flowerhead ($N = 860$). Each flower has a single ovule, which yields one seed that remains enclosed in the papryaceous calyx, the dispersal unit. Bees, bumblebees and syrphid flies are flower visitors and potential generalist pollinators (R. García-Camacho, personal observation). A dimorphic self-incompatibility system has been described for the genus *Armeria*. Populations consist of homozygous recessive (ac.ac) individuals with papillated stigmas and finely reticulated pollen grains (hereafter PAP morph) and heterozygous (AC.ac) individuals showing cob-resembling stigmas, and coarsely reticulated pollen grains (hereafter, COB morph) (Baker, 1966; Vekemans et al., 1990). In a previous survey, we observed both morphs in a 1:1 ratio in all the study populations, confirming that this species is an obligate outcrosser.

Study site—The study site in the Sierra de Guadarrama, one of the ranges of the Iberian Sistema Central, Madrid Province, Spain, receives an average of 1350 mm of annual precipitation at the Navacerrada Pass ($40^{\circ}46'N$, $4^{\circ}19'W$; 1860 m a.s.l.), concentrated from early October to late May. A strong dry season (<10% of total annual rainfall) occurs from June to September (Palacios et al., 2003; Giménez-Benavides et al., 2007a, b).

We selected four populations: two on rocky microhabitat, corresponding to the highest and lowest local altitudes for the microhabitat, and two on pasture, also at the local altitudinal limit of the species. To avoid bias, we selected well-structured populations with at least 100 mature individuals. This requirement is especially relevant for defining the lowest edge because isolated individuals or very small clusters may occur even 75–100 m below selected populations in both microhabitats. These four populations were sited in three localities (García-Camacho and Escudero, 2008). Locality 1 is a granite crag (1750 m a.s.l.) at Cuerda de los Porrones, a secondary range of Sierra de Guadarrama, surrounded by open shrubs dominated by *Cistus laurifolius*, Scots pine plantations, and graminoid dry pastures dominated by the endemic *Festuca curvifolia*. This site corresponds to the lowest edge of the species in the studied area and is the smallest, most isolated among the studied populations. Locality 2 is situated 2 km from locality 1 at Loma de Cabezas (2000 m a.s.l.), a slope running NE-SW from Guadarrama's main range above the local timberline at 1900 m a.s.l. The vegetation here is dominated by *Cytisus oromediterraneus* and *Juniperus communis* subsp. *alpina* shrubs interspersed with *Festuca curvifolia* pastures. This site corresponds to the lower edge on pasture microhabitat. Locality 3 is on the upper slopes and summit of Cabezas de Hierro Menor (2365 m a.s.l., the third highest summit of Guadarrama). At this site, we selected two close populations one for each microhabitat (rock and pasture). The vegetation is dominated by short cryophilic *Festuca curvifolia* pastures with scattered individuals of *Juniperus communis* subsp. *alpina* and *Cytisus oromediterraneus*, whereas on the rocky outcrops *Saxifraga willkommiana*, *Murbeckiella boryi*, *Sedum brevifolium*, and *Veronica fruticans* subsp. *cantabrica* are the most common species.

TABLE 1. Means \pm SD for plant density, the pollination context (PC) indices, and the components of the PC indices for each population of *Armeria caespitosa*.

Variable ^a	Population (sample size)			
	Low rock ($N = 28$)	Low pasture ($N = 28$)	High rock ($N = 36$)	High pasture ($N = 33$)
Mean distances to compatible neighbors (cm)	99.83 \pm 58.08 a	96.51 \pm 38.39 a	109.97 \pm 57.55 a	116.64 \pm 18.98 a
Mean distances to incompatible neighbors (cm)	120.09 \pm 57.56 a	114.47 \pm 56.54 a	125.39 \pm 65.46 a	118.02 \pm 22.77 a
Number of compatible flowerheads	13.39 \pm 12.58 a	22.89 \pm 35.91 ab	28.92 \pm 22.83 b	51.09 \pm 19.18 c
Number of incompatible flowerheads	12.25 \pm 9.71 a	25.96 \pm 55.08 b	26.41 \pm 21.07 b	48.52 \pm 18.02 c
Number of compatible neighbors	3.57 \pm 2.67 a	8.29 \pm 5.54 b	4.38 \pm 2.51 a	17.18 \pm 5.14 c
Number of incompatible neighbors	3.71 \pm 2.19 a	7.54 \pm 5.32 b	4.35 \pm 2.82 a	16.15 \pm 4.72 c
PC _{2m} ^b	0.52 \pm 1.06 a	0.36 \pm 0.45 a	0.88 \pm 1.65 a	0.62 \pm 0.30 a
In-PC _{2m} ^b	0.28 \pm 0.39 a	0.42 \pm 0.65 a	0.64 \pm 1.52 a	0.69 \pm 0.45 a
Density (2 m)	7.61 \pm 3.19 a	15.90 \pm 10.58 b	8.73 \pm 4.74 a	33.42 \pm 7.55 c

^a Within each row, mean values followed by different letters were significantly different ($P < 0.05$) according to generalized linear models with population as predictor and each variable as a response variable and attending to the differences in least square means, (DIFF option, LSMEANS, Genmod., SAS, version 9). Density (2 m) = number of plants within 2 m.

^b Pollination context indices (PC) describe the pollination context for a focal plant, taking into account the quantity (number of flowerheads of the surrounding conspecifics) and quality of pollen reception (morph of the conspecifics) and the probability of reception of compatible pollen (inversely proportional to the distance to the pollen donors) in the neighborhood of the plant up to 2 m from the focal plant. Different indices were calculated with the compatible (PC) and the incompatible (In-PC) neighborhoods.

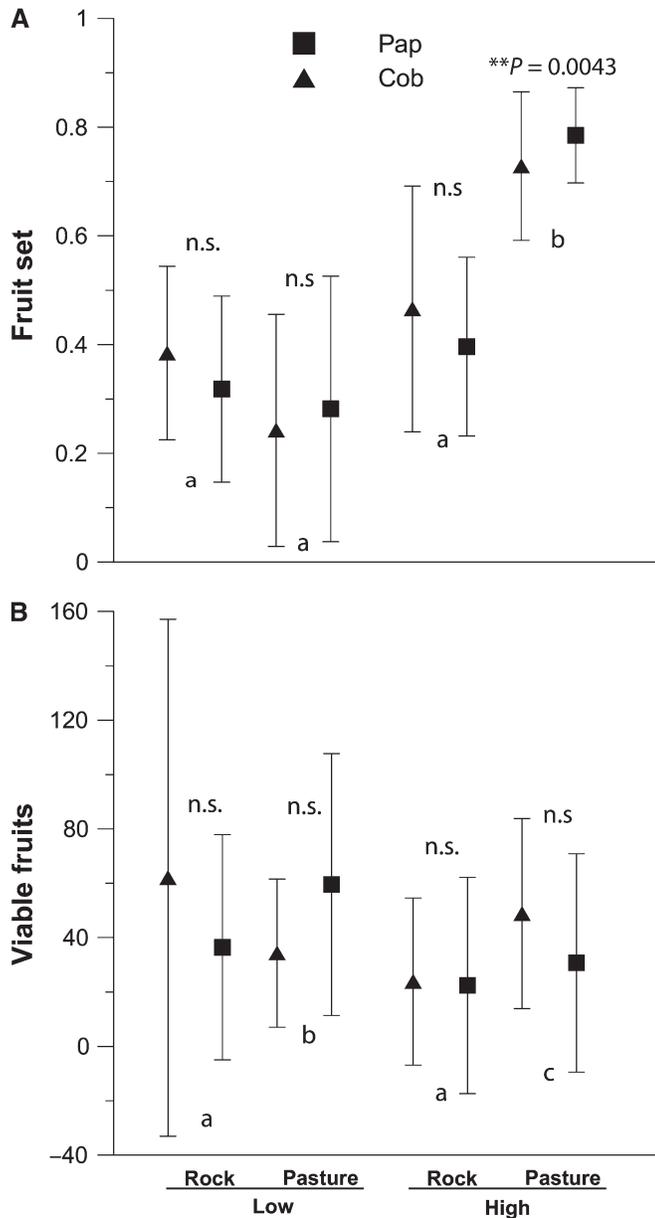


Fig. 1. Reproductive success estimates for each morph in the study populations of *Armeria caespitosa*. (A) Fruit set and (B) number of viable fruits (mean \pm SD). Significance level of the differences between morphs at each population (above plots) were obtained from the corresponding generalized linear model (GLM) (Table 3) using the DIFF option, LS-MEANS statement, Proc Genmod in SAS version 9. Between-population differences in female reproductive success estimates (letters below plots) were obtained from the corresponding GLM (Table 2) using the DIFF option, LSMEANS statement, Proc Genmod. Different letters denote a significant difference between populations.

Sampling methods—We randomly tagged individuals in 2004 in each population (García-Camacho and Escudero, 2008; also see 2006 sample sizes in Table 1) and studied their conspecific neighborhoods in 2006. To quantify the focal plants pollination context, in the 2006 flowering season, we concentrated the sampling effort during the flowering peak of each population. We scored the morph for every tagged plant and measured the distance to its conspecific neighbors flowering synchronously up to 2 m apart, identifying their morphs and counting their flowerheads. Several studies suggest that most of the pollen received by an individual plant comes from this short a distance, especially in

TABLE 2. Results of generalized linear models testing the effects of population and pollination context on (A) fruit set and (B) number of viable fruits including the data from all four populations of *Armeria caespitosa*. Models were performed using the Genmod procedure of SAS. For fruit set, we assumed a binomial error and a logit link function; for viable fruits, we assumed a Poisson error and a log link function.

	F	df	P
A) Fruit set (AIC = 322.1)			
Morph	1.66	1,115	0.20
Flowerheads (focal plant)	-0.26	1,115	0.60
Population	8.08	3,115	0.0001
PC _{2m}	+5.38	1,115	0.0221
PC _{2m} \times population	7.33	3,115	0.0001
In-PC _{2m}	+0.12	1,115	0.72
B) Viable fruits (AIC = 319.8)			
Morph	0.00	1,115	0.97
Flowerheads (focal plant)	+105.4	1,115	0.0001
Population	8.15	3,115	0.0001
PC _{2m}	+9.72	1,115	0.0023
PC _{2m} \times population	7.5	3,115	0.0001
In-PC _{2m}	+0.00	1,115	0.97

Notes: AIC = Akaike information criterion; (+, -) sign of the model estimate preceding each F value; df = numerator, denominator degrees of freedom; PC_{2m} = pollination context index (compatible neighborhood); In-PC_{2m} = pollination context index (incompatible neighborhood). Boldfaced values are significant at P = 0.05.

the case of cushion-like prostrate plants (Colling et al., 2004; Escaravage and Wagner, 2004; Ishihama et al., 2006). We could distinguish the morphs in the field using a 50 \times hand magnifier. We also noted the number of flowerheads on every tagged plant. This variable provided an accurate estimate of the floral display size (García-Camacho and Escudero, 2008). We assumed that plants displaying more flowerheads would attract more pollinators.

Our new index describes the pollination context for a focal plant, taking into account the quantity (number of flowerheads of the surrounding conspecifics) and quality of pollen reception (morph of the conspecifics) and the probability of reception of compatible pollen (inversely proportional to the distance to the pollen donors) in the neighborhood of the plant. We prefer the use of flowerheads instead of plant size because the number of flowerheads per plant is highly variable (García-Camacho and Escudero, 2008), and it is a more realistic surrogate of pollen availability in the focal plant surroundings. With these premises, PC was calculated with the following formula:

$$PC_i = \sum_{j=1}^n \frac{f_j}{d_{i-j}}$$

where d_{i-j} is the distance from focal plant i to compatible neighbor plant j (cm), f_j is the number of flowerheads of the compatible neighbor j , and n is the number of neighbors. We quantified the PC within two different neighborhoods from each focal plant, 1 and 2 m, with the indices PC_{1m} and PC_{2m} respectively. We calculated these indices only with those neighbor plants compatible with the focal plant, calculating a different set of indices (In-PC_{1m} and In-PC_{2m}) with the incompatible ones. Because of their high correlation (Spearman correlations were 0.94, P = 0.0001, for both compatible and incompatible indices), the indices from both scales provided similar results, so hereafter we provide results from the 2-m indices only. PC indices ranged from 0 onward, being 0 for a neighborhood that lacks blooming neighbors. The higher the index, the more pollen is available in the neighborhood for the focal plant. It could be argued that the effect of pollination context could be evaluated by simply testing the separate effects of each component of these indices (mean distance to compatible neighbors, number of compatible flowerheads in the close surroundings, mean distance to incompatible neighbors and number of incompatible flowerheads) (for an example, see Méndez and Díaz, 2001). However these predictors are usually highly correlated, which results in multicollinearity problems in the models. Moreover, the use of our indices would save degrees of freedom in models based on modest sample sizes and give a more integrated view of the pollination context as a whole.

At the end of the flowering season and prior to seed dispersal, we collected all flowerheads from all focal plants. For each focal plant, we counted the

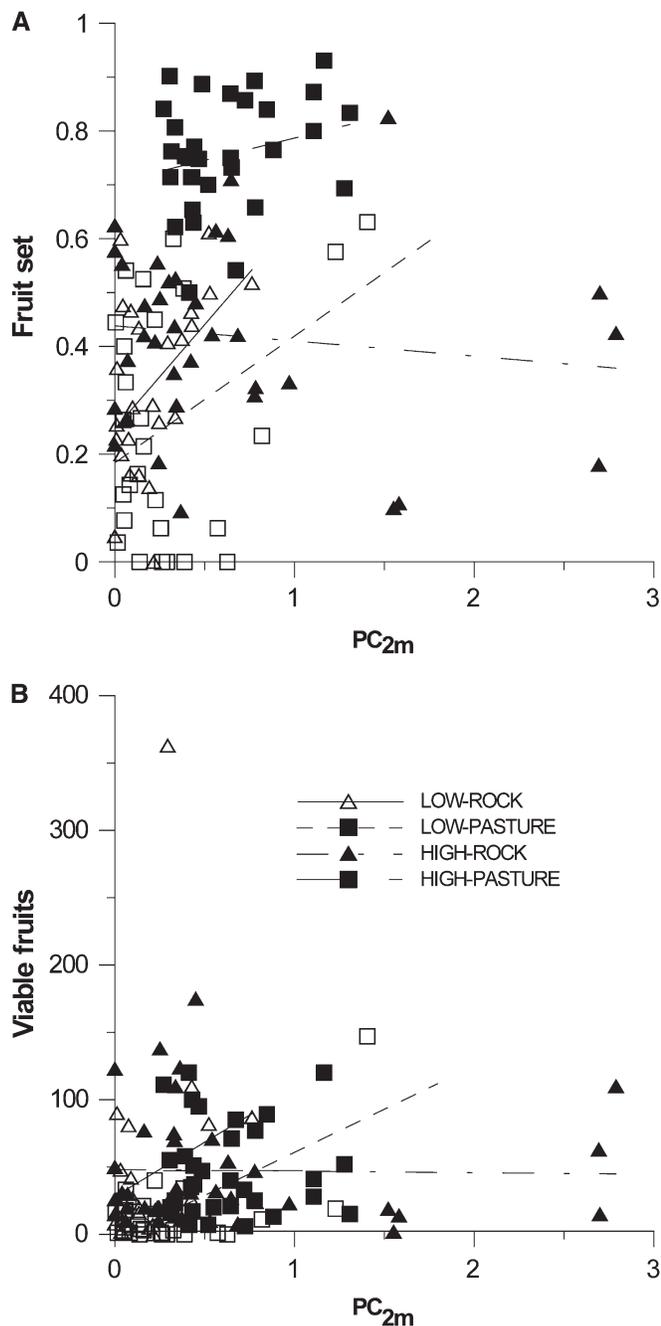


Fig. 2. PC_{2m} index against (A) fruit set and (B) number of viable fruits in populations of *Armeria caespitosa*. We provide the linear fit for each population. Table 3 gives the significances for these relations.

number of viable fruits and calculated the fruit set for the plant as the number of viable fruits divided by the total number of flowers (for more details, see García-Camacho and Escudero, 2008).

Statistical analyses—To test for between-population differences of the variables considered to calculate PC indices (see Table 1), we fitted generalized linear models (GLMs) with population as predictor and the different variables as response and checked the differences in the least squares means for each population by means of the LSMEANS and DIFF options of GENMOD (SAS version 9, SAS Institute 2002, Cary, NC, USA). For each response variable, the most suitable link function was selected.

As a preliminary step, we conducted GLMs (McCullagh and Nelder, 1989) including data from all populations. We tested the effects of PC (both compatible and incompatible) on fruit set and number of viable fruits. Aside from PC as a fixed predictor, we also included the population and interaction (population \times compatible PC; population \times number of compatible neighbors), the focal plant morph to know whether there are morph-based differences in reproductive success, the incompatible PC index to evaluate competition between compatible and incompatible pollen, and the number of flowerheads of the focal plant to include an estimate of the pollinator attractiveness of each plant. In the case of fruit set, we assumed a binomial error and used the logit link function, whereas for viable fruits we assumed a poisson error and the log link function. We also used the LSMEANS and DIFF options of GENMOD (SAS version 9) as a posthoc test to check the differences in female reproductive success among populations.

Because of the significant interactions between population and compatible PC (see Results), we conducted separate GLMs for each population. Each model included the same variables as the overall model for each response variable except population and the interaction. In the models for each population, when morph had a significant effect, we used the LSMEANS and DIFF options of GENMOD (SAS version 9) as a posthoc test to check the differences in female reproductive success between morphs. We used Akaike information criterion (AIC) to compare model fits per population including our PC indices with the model fits including number of flowerheads (compatible and incompatible) or mean distance to neighbors (compatible and incompatible) instead of the PC indices. As we compared models with equal number of predictors and fitted with the same number of cases, lower AIC values indicate the better fits (Quinn and Keough, 2003).

RESULTS

Plant density, i.e., number of plants surrounding each focal individual within 2 m, varied significantly among the study populations, as did the number of neighborhood flowerheads (Table 1). Contrarily, our estimates of PC and the mean distances to neighbors did not vary significantly among populations. Rocky populations, which had lower densities, had also more variable PC indices, although this difference was not significant. In addition, populations at the low altitude edge in both microhabitats had lower mean PC indices, although the difference was not significant.

Between-population variation in the reproductive success estimates (Fig. 1) showed higher fruit set at the higher rocky population and differences in viable fruit production between microhabitats at each altitude (Table 2, Fig. 1). The overall effect of the compatible PC across populations was significant for both fruit set and viable fruits. Moreover, the interaction population \times compatible PC was significant for fruit set and viable fruits (Table 2), suggesting that the PC effects were population-dependent. The reproductive success of populations at the low altitude edge was linearly dependent on PC, but this relation was not significant for populations at the high altitude edge for either viable seeds or fruit set (Fig. 2). In the low-rock population, fruit set was affected by PC, whereas in the low-pasture population, the number of viable fruits was predicted by PC (Table 3). Any PC effects were always positive, so plants with a more favorable neighborhood had higher fruit set or produced more viable fruits. The incompatible PC had no significant effects on either fruit set or number of viable fruits. Moreover, the number of viable fruits depended on the number of flowerheads (Table 3). Our models also showed that fruit set was morph-dependent in the high-pasture population (Table 3); Pap plants (back-transformed least-square means = 0.76–0.86) set significantly higher percentage of fruits than the Cob plants (back-transformed least-square means = 0.65–0.77) (Fig. 1A). In addition, all models that included our PC indices

TABLE 3. Results of generalized linear models testing the effects of pollination context on (A) fruit set and (B) number of viable fruits for the four populations of *Armeria caespitosa*. Models were performed using the Genmod procedure of SAS. For fruit set, we assumed a binomial error and a logit link function, whereas for viable fruits we assumed a poisson error and a log link function.

	Low rock		Low pasture		High rock		High pasture		
	F	df	F	df	F	df	F	df	
A) Fruit set									
Morph	0.01	1,23	0.19	1,23	1.06	1,32	7.50*	1,28	
Flowerheads (focal plant)	+0.38	1,23	-0.16	1,23	-2.03	1,32	-3.17	1,28	
PC _{2m}	+5.03*	1,23	+2.51	1,23	-1.75	1,32	+1.08	1,28	
In-PC _{2m}	-0.94	1,23	+0.01	1,23	+0.15	1,32	+0.42	1,28	
B) Viable fruits									
Morph	0.39	1,23	0.50	1,23	2.75	1,32	2.23	1,28	
Flowerheads (focal plant)	+45.88*	1,23	+8.57**	1,23	+26.78***	1,32	+54.79***	1,28	
PC _{2m}	+3.21	1,23	+4.33*	1,23	-0.14	1,32	+0.04	1,28	
In-PC _{2m}	-0.80	1,23	-0.17	1,23	+0.40	1,32	-0.04	1,28	

Notes: (+,-) the sign of the model estimate precedes each F value; df = numerator, denominator degrees of freedom; PC_{2m} = pollination context index (compatible neighborhood); In-PC_{2m} = pollination context index (incompatible neighborhood). $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; boldfaced values are significant at $P = 0.05$.

were better fits with the data (lower AIC values) than were models that included only the other estimates of neighborhood quality around the focal plants (Table 4). For the high-rock population, mean distance to compatible neighbors had a significant positive effect on fruit set (Table 4), although such an effect is difficult to interpret.

DISCUSSION

Our PC indices were useful to describe the conspecific neighborhood of focal plants, a quantitative measure of pollen availability in the close surroundings that provided a better fit with the data than did other estimates of neighborhood quality alone. In addition, our results support the hypothesis that the neighborhood quality influenced the reproductive success of *Armeria caespitosa*. Such pollination context effects hold true, at least, for the two populations located at the low edge in each microhabitat, the most stressed (García-Camacho and Escudero, 2008). At those sites, the conspecific neighborhood of an individual, dependent on the number, distances, and potential production of compatible pollen, was important for its reproductive success. The more numerous and closer the compatible neighbors and the higher their floral production, the higher was the fruit set and the viable fruit on a focal plant. The effects of density, another component of the neighborhood, on plant reproductive

success have been detected before at such small scales (Roll et al., 1997; Bosch and Waser, 2001; Colling et al., 2004; Spigler and Chang, 2008) and even at the population scale (Luzuriaga et al., 2006). Other results suggest that most of the pollen received by an individual plant comes from such short distances (Widén and Widén, 1990; Escaravage and Wagner, 2004; Ishihama et al., 2006). However, our PC indices provide more information than the raw measure of density, in spite of the high correlation (Density_{2m}-PC_{2m}: Spearman's $R = 0.584$, $P = 0.0001$). These indices include relevant spatial information for plant-pollinator interactions (Morales and Vazquez, 2008) and also consider the quality of the neighbors as pollen donors (Le Cadre et al., 2008). Two plants could have the same neighbor plant density, but differences in the distances to conspecific neighbors and their respective flowering displays may result in different spatial configurations and PC values. In addition, what we called incompatible PC did not affect either fruit set or number of viable fruits, likely because of a physical constraint on the pollen grains germinating on opposing stigmas, especially the coarsely reticulated ones (Richards, 1997). These results suggest that there is no intermorph pollination interference in *A. caespitosa* (Nishihiro and Washitani, 1998), contrary to other species, whose stigma is clogged by incompatible pollen (Shore and Barrett, 1984; Scribailo and Barrett, 1994; Ramsey and Vaughton, 2000) or has some degree of assortative mating in at least one morph (Stehlik et al., 2006; Van Rossum et al., 2006).

TABLE 4. Comparison between the generalized linear models based on the PC indices (same models as in Table 3) and those based on single estimates of neighborhood quality (number of flowerheads or mean distances to neighbors for four populations of *Armeria caespitosa*). Lower AIC values indicate the model with better fit.

Response variable	Main effect in the model	Low rock		Low pasture		High rock		High pasture	
		F (df = 1,23)	AIC	F (df = 1,23)	AIC	F (df = 1,32)	AIC	F (df = 1,28)	AIC
Fruit set	PC _{2m}	+5.03 *	70.1	+2.51	88.8	-1.75	96.2	+1.08	68.8
	No. compatible flowerheads	+0.00	70.9	-0.07	95.4	-0.17	97.5	+1.51	75.2
	Mean distance to compatible neighbors	-0.02	90.9	+0.47	105.7	+5.38 *	108.3	-3.03	86.7
Viable fruits	PC _{2m}	+3.21	77.3	+4.33 *	93.1	-0.14	93.5	+0.04	53.1
	No. compatible flowerheads	-1.23	79.6	+1.27	100.4	-0.36	95.1	+0.61	55.3
	Mean distance to compatible neighbors	-0.20	96.0	+1.65	111.5	+3.33	106.1	-2.85	69.0

Notes: AIC = Akaike information criterion; (+,-) the sign of the model estimate precedes each F value; df = numerator, denominator degrees of freedom; PC_{2m} = pollination context index (compatible neighborhood); In-PC_{2m} = pollination context index (incompatible neighborhood). $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; boldfaced values are significant at $P = 0.05$.

Pollen limitation may be the mechanism underlying this PC effect (Le Cadre et al., 2008). The availability of compatible pollen in the local neighborhood may constrain the reproductive success of focal plants. In this sense, PC values were not significantly lower at these edge populations, although the mean values were lower for the lowest population at each microhabitat (Table 1). Because we separated the compatible from the incompatible PC, our results are likely attributable to compatible pollen quantity limitation and not to pollinator restrictions (Aizen and Harder, 2007). *A. caespitosa* is an early-flowering plant (García-Camacho and Escudero, 2008) whose blooming does not overlap with almost any other species in the community, and it is visited by generalist pollinators. Visits are irregular at the beginning of the flowering season (Kudo, 1993; Kudo and Suzuki, 2002; Kudo and Hirao, 2006), but if the amount and diversity of pollinators is limited, then the limitation should be greater at higher altitudes (Arroyo et al., 1982, 1985; Inouye and Pyke, 1988; Totland, 1993).

It could be argued that the PC effect may be caused by a higher attraction of denser patches to pollinators (Roll et al., 1997; Bosch and Waser, 2001). If that were the only mechanism underlying the PC effects, however, it is likely that we would also have found a positive effect of incompatible PC because the morphs are not distinguishable by pollinators. Furthermore, although our observational study does not rule out possible underlying effects of microsite quality on plant reproductive success (Bosch and Waser, 2001; Colling et al., 2004), in a previous study on the same populations with the same focal plants (García-Camacho and Escudero, 2008), microsite variability did not significantly affect the reproductive success in *A. caespitosa*.

This context dependence was only present at the low edge, precisely where fruit set was significantly lower. Similar results were obtained for *Arum italicum* and explained by lower flowering synchronies at the most sparse sites (Méndez and Díaz, 2001). Although in *A. caespitosa* more synchronous plants have higher reproductive success, synchrony did not differ enough among populations (García-Camacho and Escudero, 2008) to justify the same mechanism here.

The individual floral display (number of flowerheads) only had a significant effect on the number of viable fruits. This positive effect on seed production and not on fruit set suggests a size-dependent effect not related to pollinator attraction (García-Camacho and Escudero, 2008).

We found morph-dependent differences in fruit set at the high-pasture population, where PAP individuals had higher fruit set (Fig. 2). This large, dense population also showed high PC values and the highest plant density and fruit set. Such population characteristics do not favor the persistence of intermorph differences in fecundity, more likely to occur in small isolated populations of species with weak self-incompatibility systems (Brys et al., 2008). Although our results with the incompatible PC indices suggest that the dimorphic self-incompatibility system does work in *A. caespitosa*, we cannot rule out that in some situations one morph may experience selfing, as previously observed in the genus *Armeria* in very stressful environments. Vekemans et al. (1990) found intermorph variability in reproductive success in heavy-metal tolerant populations of *A. maritima* with differences in mass allocation between morphs; the PAP morph was more female, a better selfer, and less sensitive to inbreeding depression. Given that the western Mediterranean is considered the diversification center of the genus *Armeria* (60% of the 120 species occur in the Iberian Peninsula) with a high number of species living in a wide array of

habitats (Nieto Feliner, 1990), the variability of the dimorphic self-incompatibility system that we found in *A. caespitosa* in this study and in the system in *A. maritima* outside the Iberian Peninsula may also be found in other Iberian endemic species and could help to explain the local diversity of the genus.

Our results show that the PC at subpopulation scales may profoundly affect the reproduction of *A. caespitosa*, especially at the lower edge of its altitudinal distribution. Parameters other than plant density on an individual basis are useful for the study of small-scale density-dependent processes that affect pollination success and other reproductive processes, especially if they integrate neighborhood quality information at adequate spatial scales. Furthermore, we propose that the specific role of the spatial structure of compatible vs. incompatible morphs at small scales of the dimorphic self-incompatibility system in *Armeria* deserves further attention.

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