RESEARCH PAPER

Number of conspecifics and reproduction in the invasive plant *Eschscholzia californica* (Papaveraceae): is there a pollinator-mediated Allee effect?

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ABSTRACT

The component Allee effect has been defined as 'a positive relationship between any measure of individual fitness and the number or density of conspecifics'. Larger plant populations or large patches have shown a higher pollinator visitation rate, which may give rise to an Allee effect in reproduction of the plants. We experimentally tested the effect of number of conspecifics on reproduction and pollinator visitation in *Eschscholzia californica* Cham., an invasive plant in Chile. We then built patches with two, eight and 16 flowering individuals of *E. californica* (11 replicates per treatment) in an area characterised by dominance of the study species. We found that *E. californica* exhibits a component Allee effect, as the number of individuals of this species has a positive effect on individual seed set. However, individual fruit production was not affected by the number of plants examined. Pollinator visitation rate was also independent of the number of plants, so this factor would not explain the Allee effect. This rate was positively correlated with the total number of flowers in the patches. We also found that the number of plants did not affect the seed mass or proportion of germinated seeds in the patches. Higher pollen availability in patches with 16 plants and pollination by wind could explain the Allee effect. The component Allee effect identified could lead to a weak demographic Allee effect that might reduce the rate of spread of *E. californica*. Knowledge of this would be useful for management of this invasive plant in Chile.

INTRODUCTION

The component Allee effect has been defined as 'a positive relationship between any measure of individual fitness and the number or density of conspecifics' (Stephens *et al.* 1999; Courchamp *et al.* 2008). This effect may generate a demographic Allee effect, which is a positive relationship between the overall individual fitness, usually quantified as the *per capita* population growth rate, and population size or density (Courchamp *et al.* 2008). In plants, the component Allee effect has been studied mainly in reproduction of rare species or species threatened by population fragmentation or herbivory (Silander 1978; Lamont *et al.* 1993; Widén 1993; Hackney & McGraw 2001; Leimu *et al.* 2006; Wagenius *et al.* 2007). However, the factors that explain this effect have been less evaluated (Courchamp *et al.* 2008), especially in invasive species.

In general, larger plant populations or large patches attract a higher number of pollinators (Sih & Baltus 1987; Goulson 2003; Steven *et al.* 2003). A higher pollinator visitation rate in these populations can give rise to a positive relationship between individual reproductive success and the number or density of plants of the same species (Ågren 1996; Groom 1998; Forsyth 2003; Ward & Johnson 2005). This relationship

would hold until a threshold population size is reached, above which intraspecific competition for pollinator services may become more important than facilitation (Feinsinger 1987; Hegland *et al.* 2009). The size of plant populations may also affect the quality of pollen transferred to plants. Pollen quality may be lower in small populations, since pollen transfer would occur mainly between related individuals. This could result in biparental inbreeding depression (Ellstrand & Elam 1993). Additionally, smaller populations have shown a higher level of self-fertilisation, which can lead to uniparental inbreeding depression (Raijmann *et al.* 1994; Courchamp *et al.* 2008). Due to the effects of inbreeding depression, seeds from small populations may have a lower germination percentage and lower mass than seeds from larger populations (Menges 1991; Heschel & Paige 1995; Naito *et al.* 2008; Collin *et al.* 2009). This corresponds to a genetic Allee effect (Courchamp *et al.* 2008).

The Allee effect has been identified in the reproduction of some exotic and invasive plants that show lower seed production per fruit and reduced germination rate in individuals from small populations (Cappuccino 2004; Elam *et al.* 2007). However, these studies have not evaluated whether pollinator activity can lead to an Allee effect, although the reproduction of many exotic plants depends on mutualistic pollinators

(Richardson *et al.* 2000). Further study of factors affecting the reproduction of invasive plants would be useful for management of these organisms, which may cause a large loss of biodiversity (Richardson *et al.* 2000).

In this study, we tested the effect of the number of *Eschscholzia californica* plants on reproduction of conspecifics and pollinator visitation in central Chile. *E. californica* is an exotic species and described as an invasive plant in Chile (Arroyo *et al.* 2000; Leger & Rice 2003). The species is native to western North America, where it is mainly insect-pollinated (Cook 1962). Cook (1962) also stated that *E. californica* presents anemophily; however, the importance of this type of pollination has not been evaluated. In populations of *E. californica* from central Chile it was determined, through a pollinator exclusion experiment, that seed production depends on pollinator activity (Arredondo-Núñez 2011). Furthermore, it was found that individuals of *E. californica* in populations from Chile and California (USA) are mostly self-incompatible (Cook 1962; Leger & Rice 2007), and that those having a degree of self-compatibility produce more seeds with cross-pollination than with self-pollination (Cook 1962; Arredondo-Núñez 2011).

Specifically, we addressed the following questions: (i) is there an Allee effect in *E. californica* reproduction (fruit and seed production); (ii) what is the effect of the number of *E. californica* individuals on the quality of seeds (mass and germination) in conspecifics; and (iii) what is the effect of the number of *E. californica* individuals on pollinator visitation rate?

MATERIAL AND METHODS

Study species

Eschscholzia californica (Papaveraceae) is an invasive perennial herb in Chile (Quiroz *et al.* 2009). The nectarless flower has a varying corolla diameter (1.6–7.6 cm), filiform style and numerous stamens (Villagrán *et al.* 2007). The flower lasts 5 days, closing at night, and also in the daytime if it is raining or cloudy (Villagrán *et al.* 2007). The species reproduces through seeds. The fruit is a pod with explosive dehiscence, which leads to ballistic seed dispersal (*e.g.* Garrison *et al.* 2000). The habitat of this species in Chile is mainly vacant lots and disturbed grasslands (Quiroz *et al.* 2009).

Study area

Research was conducted on a private farm property located in Santo Domingo (33°52′ S, 71°35′ W), V Region, in central Chile. This site is at 115 m a.s.l. and is characterised by the dominance of *E. californica*. Other species observed at lesser frequencies were *Chrysanthemum coronarium* (exotic), *Verbascum virgatum* (exotic), *Rubus ulmifolius* (exotic and invasive), *Muehlenbeckia hastulata* (native) and *Rumex* sp. (exotic). The study area has a pluviseasonal mediterranean bioclimate (Luebert & Pliscoff 2006).

Dependence on pollinators for seed production

We performed a pollinator exclusion experiment in an *E. californica* population to assess whether seed production of individuals of this species in the study area depends on animal pollination. In November 2010, during the peak of the *E. californica* flowering period 65 plants of this species, located at least 2 m apart, were randomly selected. We then made a random selection of two flowers in pre-anthesis (flower buds) from each of these plants. On each selected individual, one flower was assigned to a pollinator exclusion treatment and covered with a semi-transparent bag of tulle netting. The other selected flower (control) was marked with a thread and remained exposed to pollinators. In December 2010, the fruits of each of the two selected flowers were collected in order to quantify the number of seeds per flower.

Experimental setup

We evaluated the effect of the number of *E. californica* individuals in bloom on reproduction of conspecifics and pollinator visits using a manipulative field experiment. At the study site, an experiment was set up in November 2010, consisting of *E. californica* patches. Flowers within each patch were removed to create the following treatments of number of *E. californica* individuals in bloom: (i) two individuals; (ii) eight individuals and (iii) 16 individuals. A total of 33 experimental units were defined, and the treatments were assigned at random to produce a completely randomised design (Hurlbert 1984; Underwood 1997). Each treatment was replicated in 11 patches, and the patches consisted of pre-existing individuals in the study area. The patches were located 14 m apart in order to minimise pollinator response being affected by adjacent patches (*e.g.* Elliott & Irwin 2009). It has been shown, in experiments with patches of plants more than 10 m apart, that some bee species prefer visiting certain patches, which consequently restricts pollen flow (Osborne & Williams 2001).

To separate the treatments, *E. californica* flowers were cut in a radius of 14 m around each experimental patch. The plants, however, were not removed in order to avoid altering any potential intraspecific competition for water or nutrients, as this could affect seed production (Wallace & O'Dowd 1989). Flowers of heterospecific individuals around and within each patch were also removed. For each experimental patch, we counted the total number of open flowers (in anthesis) during 1 day, and measured the spacing between individuals (density *sensu stricto*), since these factors can influence pollinator visits (Kunin 1997). The total number of open flowers was considered a proxy for pollen availability in the experimental patches.

To measure spacing between individuals, we calculated the average distance to the nearest neighbour (individual with flowers) for each patch. In the two-plant and eight-plant patches, the distance to the nearest neighbour was measured for each individual, and in the 16-plant patches, this distance was measured for eight randomly chosen individuals. We also measured the length and width of each experimental patch. To quantify the spacing between individuals, we calculated the Clark & Evans (CE) aggregation index for each patch as

$$CE = \left(\sum r/N\right)/(1/2\sqrt{\rho}) \tag{1}$$

where N = number of measurements of distance taken in the observed sample, r = distance from a given individual to its nearest neighbour, and ρ = number of individuals per unit area. This index measures whether individuals are clustered or

distributed randomly (Clark & Evans 1954). In a random distribution, CE = 1, and under conditions of maximum aggregation, CE = 0 (Clark & Evans 1954). We calculated floral display as the mean number of flowers per plant over a period of 17 days. This measure was considered a proxy for plant size.

Pollinator visitation rate

Pollinator visitation to *E. californica* individuals and their identity were recorded for each experimental patch during 17 sunny days in November 2010. We kept flowers surrounding the patch cut during this period. We considered a visit to be an event when a visitor landed on an open flower and had contact with the stigma and/or anthers. Our pollinator observation methodology was similar to that of Muñoz & Cavieres (2008). There were four 10-min observation periods per hour. Observations began between 10:15 and 11:50 h, and ended between 16:30 and 17:00 h, depending on weather conditions, which affected flower opening and closing. Pollinator visitation rates were calculated as (number of pollinator visits/number of open flowers per plant) per 10 min. For each patch, we calculated the average pollinator visitation rate. The mean observation time per focal plant (N = 143) was 3 h 16 min. We accumulated a total of 2714 10-min observations. In the patches with two plants, pollinator visits to one individual were recorded, while in the patches with eight and 16 plants, pollinator visits to four and eight randomly selected focal individuals, respectively, were recorded. Patches with 16 plants were divided into two areas, in which pollinator visits to four focal individuals were observed simultaneously. Three observers recoded the pollinator visits. For each focal plant, records of visits were made for each hour during the observation period. Insects from the families Coccinellidae and Scarabaeidae (Coleoptera), Muscidae (Diptera) and hemipterans were excluded from the analysis because they did not make contact with flower sex organs.

Fruit and seed production

Fruit production and the number of seeds per fruit were quantified from individuals in the experimental patches. To do so, the same focal individuals used to record pollinator visits were selected from the eight-plant and 16-plant patches. Two additional individuals from the 16-plant patches were also selected, since these patches could have more data variability, which might reduce statistical power. Ten flowers in pre-anthesis were randomly chosen from among the selected individuals in the eight-plant and 16-plant treatments, and from both individuals in the two-plant patches. These flowers were marked with sewing thread during the first half of the pollinator visits recording period (day 3 and day 7). During the second half of December 2010, the mature fruits (pods) produced by the marked flowers were collected, placed in individual paper bags and stored in the dark at ambient temperature. Some pods that were damaged and partially destroyed (presumably by birds) were not included in the seed count. For each selected plant, we calculated fruit set as the number of fruits produced divided by the number of marked flowers. We also calculated individual mean seed production per fruit. In addition, we quantified the proportion of aborted seeds per fruit as [number of aborted seeds/(number of mature seeds + number of aborted seeds)].

Germination and seed mass in patches of differing size

To calculate the average seed mass per fruit, four or five pods were selected from one individual from each two-plant patch, and the same number of fruits was selected from nine individuals from each 16-plant patch (except for two replicates, from which five individuals and six individuals were selected). Three to five pods were harvested from four or five individuals from each eight-plant patch. The pods were stored in a dry location for 5 months and their seeds were then counted and weighed on a HiTech analytical balance (±0.0001 g precision).

We determined the proportion of germinated seeds by treatment as follows. We made a random selection of two to six pods from both individuals in the two-plant patches. Three or four individuals were randomly selected from each eight-plant patch, and two to five pods from each selected individual. Five individuals were randomly chosen from each 16-plant patch, and two or three pods from each selected individual. Five seeds were selected for germination from each selected pod and placed on moist filter paper in Petri dishes, which were then placed in a growth chamber in darkness at 20 °C, which are the conditions required for *E. californica* seed germination (Cook 1962). The radicle generally emerges in 3–6 days, but some seeds may take longer (Cook 1962). Because of this, we counted the number of germinated seeds by treatment every 2 or three 3 for three consecutive weeks, at which point germination had ceased.

We calculated the product of fruit set, seed set and seed germination as a measure of post-emergent reproductive success (Wiens *et al.* 1987).

Statistical analyses

We used generalised linear models (GLM) to analyse the effect of number of conspecifics in bloom on pollinator visitation rate, seed production per fruit, fruit set, seed mass, proportion of germinated seeds, proportion of aborted seeds per fruit and post-emergent reproductive success. Variables calculated as proportions (fruit set, germination and aborted seeds per fruit) were analysed using binomial distributions of errors.

We examined the relationship between spacing among individuals (CE aggregation index) in the patches and the variables pollinator visitation rate, fruit production and seed production per fruit using Spearman correlation analyses. We also examined the relationship between these variables and the total number of open flowers per patch using Spearman correlation analyses. We analysed the relationship between floral display and the proportion of germinated seeds per plant using the same correlation analysis. We used one-way ANOVA to examine the effect of number of plants on number of open flowers per patch.

In cases where the data did not show normality in spite of the appropriate transformation, nonparametric tests were performed (Wilcoxon test). GLM and Spearman correlation analyses were implemented using the language and environment for statistical computation R (R Core Team 2014). Other statistical analyses were performed using the software STATISTICA 12 (StatSoft Inc., Tulsa, OK, USA).

RESULTS

Pollinator composition in patches with different numbers of plants

A total of 14 species of insect pollinator belonging to four orders and seven families were identified as having visited *E. californica* flowers. The most represented families were Apidae (four species) and Halictidae (four species). The most abundant pollinator observed in patches with two, eight and 16 plants was *Apis mellifera* (Table 1), accounting for 94.1% of total visits recorded (2724). The second most frequent species was *Arthrobrachus nigromaculatus* (Coleoptera: Melyridae) with 4.2% of the total number of recorded visits. There were a few visits by pollinators in the orders Lepidoptera and Diptera (0.2% and 0.1% of total visits recorded, respectively).

Table 1. Taxonomic composition of pollinator visits in *Eschscholzia californica* patches with two, eight and 16 plants. Indicated is the number of visitors by family (N), percentage (%) of total number of visits by treatment and abundance of the dominant pollinator (*Apis mellifera*).

| | number of flowering plants | | | | | |
| | 2 | | 8 | | 16 | |
	N	%	N	%	N	%
Hymenoptera						
Apidae	159	88.3	755	93.8	1657	95.2
Apis mellifera	159	88.3	754	93.7	1651	94.9
others			1	0.1	6	0.3
Halictidae	3	1.7	4	0.5	10	0.6
Colletidae	3	1.7	3	0.4	1	0.1
unidentified	1	0.55	5	0.6		
Coleoptera						
Melyridae	13	7.2	34	4.2	68	3.9
Diptera						
Syrphidae					2	0.1
Lepidoptera						
Nymphalidae	1	0.55	4	0.5		
Hesperiidae					1	0.1
total	180	100%	805	100%	1739	100%

Effect of number of plants on pollinator visitation and reproductive success

Pollinator visitation rate (assembly) was not affected by the number of *E. californica* individuals examined (Fig. 1A, Table 2). The spacing between plants, or density *sensu stricto*, was not significantly correlated with pollinator visitation rate ($r_s = 0.27$, n = 33, $P = 0.124$). Fruit set did not vary significantly among treatments (Fig. 1B, Table 2) and was not significantly correlated with the spacing between plants ($r_s = -0.12$, n = 33, $P = 0.504$). Seed production per fruit varied significantly among treatments (Fig. 1C, Table 2). It was significantly higher in patches with 16 plants than in patches with two (Tukey test, $P = 0.014$; Fig. 1C) or eight plants (Tukey test, $P < 0.001$; Fig. 1C). Seed production did not differ between treatments of two and eight plants ($P = 0.244$; Fig. 1C). Seed production per fruit was not significantly correlated with the spacing between plants ($r_s = 0.02$, n = 33, $P = 0.907$). The proportion of aborted seeds per fruit was not different among treatments (Table 2); it was low in all treatments (means $\leq 3\%$). Postemergent reproductive success (the product of fruit set, seed set and seed germination) was not affected by the number of plants examined (Table 2).

The total number of flowers per experimental patch varied significantly with the number of plants examined (ANOVA: $F_{2,30} = 72.126$, $P < 0.0001$); it was significantly higher in patches with 16 plants than in patches with two (Tukey test, $P = 0.0001$) or eight plants (Tukey test, $P = 0.0006$). Mean pollinator visitation rate was positively and significantly correlated with the total number of open flowers per patch ($r_s = 0.375$, n = 33, $P = 0.031$; Fig. 2A) and with the mean number of open flowers calculated based on half the plants per patch ($r_s = 0.376$, n = 33, $P = 0.032$). The total number of open flowers was positively and significantly correlated with the mean number of open flowers ($r^2 = 0.85$, r = 0.92, n = 33, $P < 0.0001$). Fruit production ($r_s = 0.51$, n = 33, $P = 0.003$) and the number of seeds per fruit ($r_s = 0.41$, n = 33, $P = 0.018$) were also positively and significantly correlated with the total number of open flowers per patch (Fig. 2B,C).

Table 2. Analysis of deviance for GLM fits. Each response variable was modelled as a function of the number of plants per patch and significance tested against its intercept only model (null model).

| | null | | number of plants | | | |
| | residual | | residual | | | |
Response variable	df	deviance	df	deviance	F value	P value
pollinator visitation rate[a]	30	0.056	32	0.06	1.063	0.358
fruit set[b]	32	2.983	30	1.954	0.515	0.598
seed production per fruit[a]	32	27079.7	29	1257.6	198.5	<2.2e^{-16}
aborted seeds per fruit[b]	32	1.104	30	0.940	0.082	0.921
seed germination[b]	32	4.753	30	4.581	0.086	0.918
seed mass[a]	32	0.630	30	0.622	0.184	0.833
postemergent[a] reproductive success	32	552.7	30	530.1	0.640	0.535

df = degrees of freedom.
[a]Gaussian error structure.
[b]Binomial error structure.
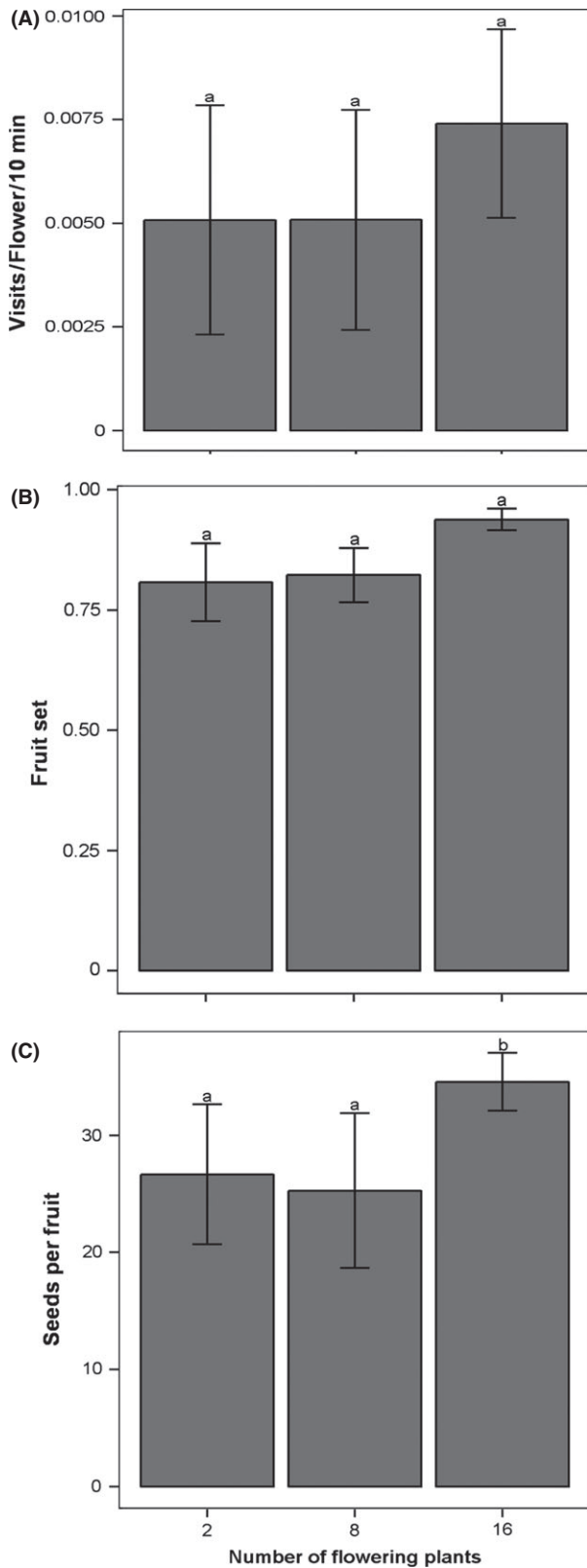
Fig. 1. (A) Pollinator visitation rate, (B) fruit production and (C) number of seeds per fruit (means ± 2 SE) in *Eschscholzia californica* patches containing different numbers of plants. Different letters above error bars indicate statistically significant differences between means at *P* < 0.05.
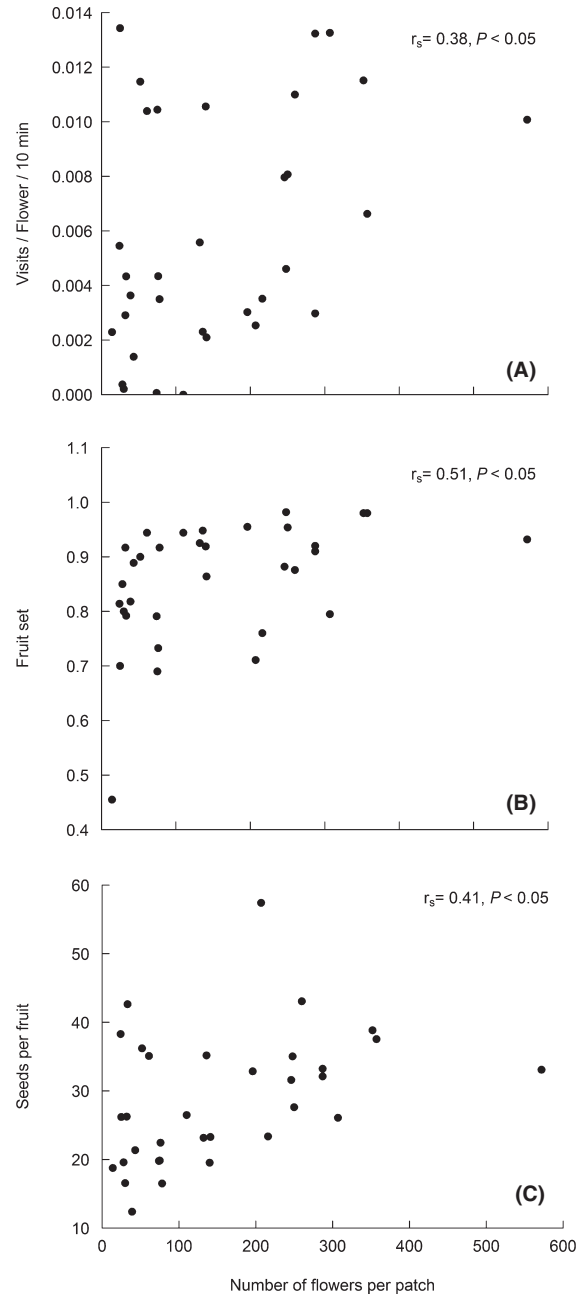

Fig. 2. Relationship between total number of open flowers in *Eschscholzia californica* patches (N = 33) and (A) mean pollinator visitation rate, (B) mean fruit production and (C) mean number of seeds per fruit. Spearman correlation coefficients (r_s) are shown.

The mean pollinator visitation rate per plant was not significantly correlated with fruit production ($r_s = 0.07$, n = 135, $P = 0.429$) or the number of seeds per fruit ($r_s = 0.15$, n = 123, $P = 0.094$).

Effect of number of plants on seed quality

The number of plants examined did not affect the proportion of germinated seeds and seed mass (Fig. 3, Table 2). The size of the plant (measured as mean number of flowers) was not
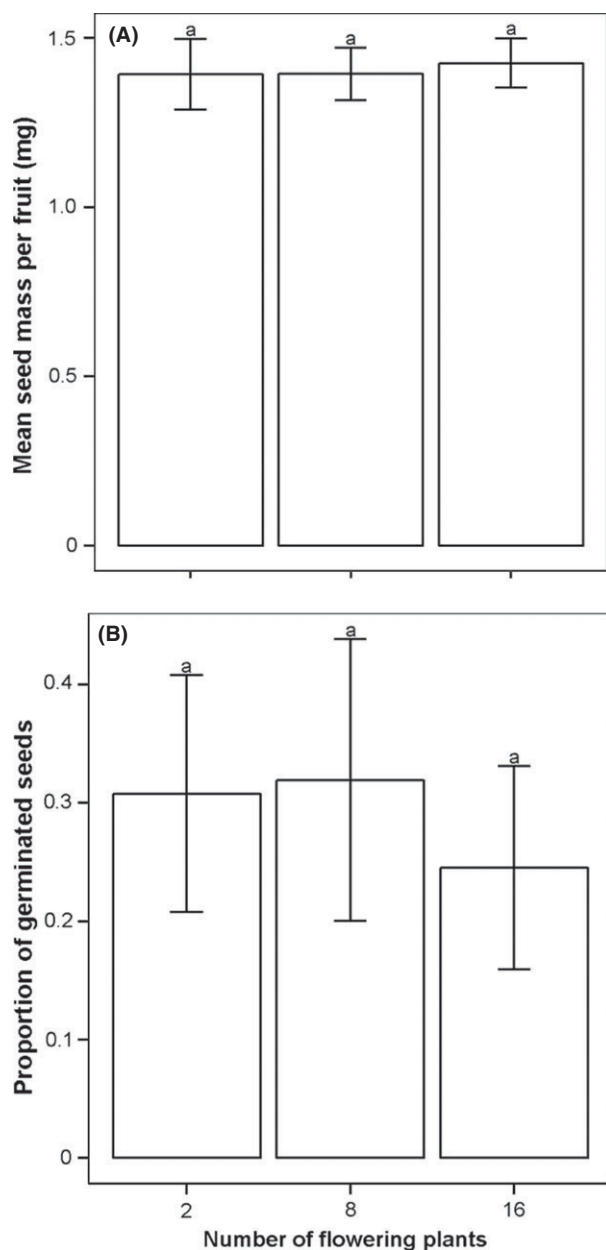
Fig. 3. (A) Mean seed mass per fruit and (B) proportion of germinated seeds (means ± 2 SE) in *Eschscholzia californica* patches containing different numbers of plants. Treatments sharing the same letter do not differ significantly (*P* > 0.05).

significantly correlated with the final proportion of germinated seeds per plant ($r_s = -0.04$, n = 83, *P* > 0.05).

Dependence on pollinators for seed production

Fruit set (number of fruits/number of flowers) in the pollinator exclusion treatment was 30.8%, while in the control group it was 92.3% (n = 52 flowers). The mean seed production per flower in the natural pollination treatment was 41.1 ± 26.0 seeds. This was significantly lower for flowers subjected to pollinator exclusion treatment (Wilcoxon test, Z = 6.02, *P* < 0.05); in fact these flowers hardly produced any seeds (mean = 1.4 ± 3.0).

DISCUSSION

This study shows that there was a component Allee effect in our experimental *E. californica* populations, since the number of conspecifics had a positive effect on individual seed production. Seed production per fruit was significantly higher in patches with 16 plants and was not different between treatments with two and eight plants per patch. However, the individual fruit production was not affected by the number of plants of *E. californica* used. Pollinator visitation rate was also independent of the number of plants, so the component Allee effect could not be attributed to pollinator visitation rate. We found a trend of higher pollinator visitation rate in the patches with 16 plants, which suggests further study of larger *E. californica* patches, which might be more attractive for pollinators. Studies conducted in other plant species have also found that pollinator visitation is not related to the number of conspecific plants in patches (Jennersten & Nilsson 1993; Kunin 1997; Cappuccino 2004). Pollinator visitation may be dependent on other variables, such as the number and/or density of flowers in patches (Heinrich 1979; Hegland & Boeke 2006), as in our study, where pollinator visitation rate was positively correlated with the total number of open flowers in experimental patches.

The calculated visitation rates are low (*e.g.* Steven *et al.* 2003; Torres-Díaz *et al.* 2011), but mean fruit set is high (80–95%). This suggests either an insufficient sample effort for pollinator visitation or very effective pollinator visits. However, pollinator visitation rate was not correlated with fruit production or seed number per fruit in our study. This could be explained by the lack of correlation between pollinator visitation rate and conspecific pollen receipt (*e.g.* Waites & Ågren 2004; Elliott & Irwin 2009). Pollen receipt could also depend on wind pollination, as described for other insect-pollinated species (Goodwillie 1999). It will be necessary to measure conspecific pollen receipt to obtain a better idea of the influence of pollinators and wind on *E. californica* reproduction in the study area.

Our pollinator exclusion experiment in an *E. californica* population showed that seed production requires pollinator visitation. However, this exclusion experiment, as well as others (*e.g.* Muñoz & Cavieres 2008; Vale *et al.* 2011), does not exclude the possible effect of wind pollination on fruit and seed production (*e.g.* Goodwillie 1999). Cook (1962) states that anemophily in *E. californica* could be facilitated by the large amount of pollen produced by the flowers and size of the pollen grains (29–55 × 29–36 μm), which is similar to that of other wind-pollinated species (Heusser 1971).

We found a positive effect of number of plants on both total number of flowers in the *E. californica* patches and seed production. However, pollinator visitation rate was independent of the number of plants. Also, there was a positive correlation between seed production and the number of flowers per patch (a proxy for pollen availability). Based on this, we propose that a factor explaining the component Allee effect could be the higher pollen availability in patches with more plants, and transfer of pollen to these plants mainly *via* wind. However, this must be evaluated experimentally.

It has been described that stigmatic pollen receipt in wind-pollinated plants is affected by pollen availability at the population level (Wilcock & Neiland 2002). Hence, a study in natural populations of an anemophilous species found a positive relationship between pollen availability in populations and

reproductive variables, such as proportion of ovules pollinated and seed set (Allison 1990). This relationship accounts for Allee effects described in the reproduction of wind-pollinated species (Nilsson & Wästljung 1987; Davis *et al.* 2004a,b).

Stigmatic pollen receipt is also affected by distance between individuals in populations in both anemophilous species (Allison 1990) and entomophilous species (Kunin 1997). For example, in anemophilous species of the genus *Thalictrum*, an increase in the distance to the nearest conspecific causes a decrease in seed production in individuals from populations with a low number of plants per unit area (Steven & Waller 2007). In our study, spacing or distance among individuals (mean = 30 ± 23 cm) did not affect fruit and seed production. This indicates that the effect of the number of *E. californica* individuals on the reproductive variables measured was independent of spacing between plants in the experimental patches.

The number of plants in the *E. californica* patches had no effect on seed mass or germination. This indicates that for our patch sizes, *E. californica* does not show a genetic Allee effect in relation to seed quality. Seedling growth and adult performance should be measured to determine whether a genetic Allee effect is expressed in later stages of the life cycle. The lack of a genetic Allee effect could be explained by pollen dispersal occurring mainly between plants of the same patch, which are more likely to be related individuals, because of ballistic seed dispersal in *E. californica*. This would not account for the large differences in quality of the received pollen, especially if plant relatedness did not differ greatly among patch sizes. Pollen dispersal could be through wind and by *Apis mellifera* (the dominant pollinator), a pollinator with a tendency to move to the nearest plant (Morris 1993). *A. mellifera* foraging ranges from 45 m to 5983 m (Núñez 1982; Hagler *et al.* 2011), and these bees might move from source to source when they forage, suggesting a potential for long-distance pollen dispersal (Hagler *et al.* 2011). Since the visitation rate of *A. mellifera* did not differ among patches with different numbers of plants, the probability of receiving pollen from *E. californica* individuals from other areas in the region could be similar among patches.

This might be another factor explaining the absence of a genetic Allee effect.

The size of *E. californica* plants in the experimental patches had no significant effect on the proportion of germinated seeds per individual. This suggests that seed germination was not influenced by maternal environmental conditions (Roach & Wulff 1987).

The number of plants examined did not affect post-emergent reproductive success (the product of fruit set, seed set and seed germination), suggesting that number of plants probably did not account for differences in per capita population growth rate between natural populations. However, in the disturbed environments where *E. californica* occurs in Chile, an Allee effect in seed production could give rise to a lower per capita population growth rate in small populations, since these populations could be more sensitive to environmental stochasticity (Boyce 1992). This could lead to a weak demographic Allee effect, because there was no large reduction in seed set in the small experimental populations. This effect could decrease the rate of spread of *E. californica* (Taylor & Hastings 2005). Such information would be useful for management of this invasive species in Chile.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Estimates and SE of GLM parameters for the factor number of plants per patch.

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