Spatial isolation impacts pollinator visitation and reproductive success of a threatened self-incompatible Mediterranean tree

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ABSTRACT

Pollination service is crucial to achieve successful plant sexual reproduction and long-term population persistence. This pollination service can be affected by plant conspecific density and also by intrinsic features of individuals related to their flowering phenology and floral display. However, studies examining intrinsic and extrinsic traits on pollinator visitation and reproductive success of Mediterranean trees with limited reproduction are still scarce. We analyzed the effects of plant isolation, flowering phenology, flower weight and tree size on flower visitation probability, flowering patch visitation probability, fruit set and crop size. To this end, we intensively monitored pollinator visitation and fruit production of 67 (in 2019) and 73 (in 2020) *Pyrus bourgaeana* Decne trees within a threatened Mediterranean population. Our results revealed that isolated individuals received more pollinators than those on conspecific aggregations, suggesting intraspecific competition for pollinators in dense flowering neighborhoods. However, fruit set was higher in trees close to flowering conspecifics despite having fewer visits from pollinators, suggesting pollen limitation but not pollinator limitation in spatially isolated trees. Interestingly, we found increased crop sizes in spatially isolated trees which could be related to reduced intraspecific competition for resources in low-density neighborhoods (water, nutrients) and/or to higher reproductive investment (i.e. higher flower production). Overall, our results indicated pollen but not pollinator limitation in spatially isolated trees. Under this scenario of sexual reproduction mediated by pollinators, our findings stress the relevance of individuals' spatial distribution for self-incompatible trees exhibiting low individuals' densities.

1. Introduction

Most angiosperm plants are pollinated by animals and this pollination service is essential to achieve plant successful sexual reproduction and long-term population persistence (Knight et al., 2005; Ollerton et al., 2011). Within plant populations, flowering individuals do not typically exhibit either uniform spatial distribution or identical phenological stage, which lead to a heterogeneous spatiotemporal distribution of floral resources. Pollinators often respond to such heterogeneity by optimizing their foraging behavior to maximize the reward obtained (MacArthur and Pianka 1966; Charnov 1976; Jha and Kremen 2013; Pope and Jha 2018). These changes in pollinators' foraging behavior being able to select the most rewarding patches and individual plants may drive differences among plant individuals in pollination failure and

reproductive success (Knudsen and Tollsten 1993; Kremen et al., 2007).

From an ecological perspective, the density of flowering plants becomes critical when the distance between conspecific neighbors leads changes in pollinators' foraging behavior (Ghazoul 2005). In addition, pollinators frequently change their foraging behavior depending on flower density, foraging more intensively in dense flowering patches due to decreased energy investment in inter-patch movements (Jha and Kremen 2013; Kacelnik et al., 1986; Dreisig 1995). Consequently, plants growing isolated and/or at low densities may experience difficulties in attracting pollinators and exhibit increased pollination failure (Kunin 1997; Waites and Ågren 2004; Castilla et al., 2015; Fedriani et al., 2015). Alternatively, increased competition for pollinators in dense flowering neighborhoods can lead to a reduction in the pollinator visitation rates and therefore, to a potential decrease of the plant reproductive success

(Mustajärvi et al., 2001; Gunton and Kunin 2009; Żywiec et al., 2018). For instance, Żywiec et al. (2018) found a lower individual reproductive success with increasing density of highly genetically related conspecifics in a long-term study with *Sorbus aucuparia*.

Plant phenological patterns are typically plastic, changing with both biotic and abiotic factors across space and time (Nicotra et al., 2010; Inouye et al., 2018). Therefore, the availability of floral resources will depend on the phenological stage of the population (Pope and Jha 2018). Those individuals flowering during the population peak might have an advantage compared with asynchronous individuals by at least two complementary reasons. First, a greater floral offer during the population peak may attract more pollinators increasing thus, the visitation rates (Forsyth 2003); and second, the higher availability of pollen donors may lead to increased pollination quantity and quality (Paschke et al., 2005; Alonso et al., 2012; Hildesheim et al., 2019). On this matter, several studies in Mediterranean plants showed that early-flowering plants are less pollinated due to the low presence of pollinators (Traveset 1995; Picó and Retana 2000; Sánchez et al., 2012) whereas late-flowering plants are more exposed to drought events, investing therefore less resources in reproduction (i.e. less amount of nectar and pollen, less flowers and more fruit abortions; Herrera 1992; Giménez-Benavides et al., 2007). On the contrary, it has been also showed that early-flowering plants can have greater reproductive success (Munguía-Rosas et al., 2011; Ison et al., 2018). For instance, Ison and Wagenius (2014) found that early-flowering individuals of *Echinacea angustifolia* showed greater reproductive success. Additionally to the spatiotemporal distribution of phenology, there are also intrinsic traits to the individual (related to reward levels offered to pollinators) that can alter these spatial and temporal dynamics. For instance, flower color, corolla size, nectar guides or scents (Endress 1994; Yan et al., 2016) can lead pollinators to learn what floral traits they prefer and thus, change their foraging behavior (Weiss 2001; Yan et al., 2016; Herrera 2020).

In this study, we investigate whether tree isolation and intrinsic traits of individuals such as flowering phenology, flower size and tree size affect pollinator visitation rates and reproductive success (i.e. fruit production) in the insect-pollinated and self-incompatible *Pyrus bourgaeana*. This locally threatened species in the Doñana area (SW Spain) (Fedriani et al., 2020a) provides crucial food resources to diverse animal guilds (Żywiec et al., 2012; Garrote et al., 2018; Selwyn et al., 2020). This tree typically occurs at low density forming spatial clusters across the landscape formed by 6–8 reproductive trees at short distances (approx. 25m; Fedriani et al., 2010). A previous study showed that a greater conspecific density can positively influence fruit initiation, but also that abortion increased with such conspecific density rates as fruit development progresses. Nevertheless, crop size was positively correlated with tree neighborhood density (Fedriani et al., 2015). Such increased fruit abortion can be at least partially driven by high inbreeding load, due to exceeded kinship at the immediate neighborhood of trees (Castilla et al., 2019a). It is not yet clarified whether differences in pollinator visitation patterns among *P. bourgaeana* trees contribute to such density-dependent relationship of tree reproductive success. Because *P. bourgaeana* is a self-incompatible species, we predicted that trees close to neighbors will receive more compatible pollen and thus will have higher reproductive success than spatially isolated trees, although that the effects of conspecific proximity could vary with the quantified aspect of reproductive success (e.g. crop size *vs*. fruit set; Fedriani et al., 2015). Also, based on previous studies (Endress 1994; Yan et al., 2016), we expected that larger flowers and trees will have higher pollinator visitation rates and thus higher reproductive success because they offer an increased floral reward to pollinators. Finally, we expected that proximity to flowering conspecifics (Fedriani et al., 2015; Żywiec et al., 2018) and flowering synchrony (Traveset 1995; Ison and Wagenius 2014) would affect pollination visitation and tree reproductive success; however, we did not anticipate any direction in such effects given the mixed results of previous studies.

2. Material and methods

2.1. Study system

Pyrus bourgaeana Decne (Rosaceae), the Iberian pear tree, is a small tree (3–6 m tall) distributed across the southern Iberian Peninsula and northern Morocco (Aldasoro et al., 1996). Our study population (called Matasgordas) is located in Doñana National Park (37°89′N, 6°26′W), on the west bank of the Guadalquivir River in southwestern Spain. The climate is Mediterranean sub-humid, characterized by dry, hot summers (June–September) and mild, wet winters (November–February). In the Doñana area, *P. bourgaeana* appears at low densities (usually <1 tree/ha) across the landscape with tree distribution varying from highly isolated to strongly aggregated. In Matasgordas, trees form spatial clusters with an average radius of 25 m (6–8 reproductive individuals; Fedriani et al., 2010). This spatial aggregation arises from dispersal limitation, spatial aggregation of dispersed seeds, and clonal growth (Fedriani et al., 2010; Fedriani and Wiegand 2014; Castilla et al., 2019b). In 2019, we used the study plot set by Fedriani et al. (2010) with an area of 60 ha (N = 67 trees) which was increased to 70 ha (N = 73 trees) in 2020 (Fig. A1). All trees were georeferenced.

The Iberian pear tree is a self-incompatible species that blooms during February–March. Flowers are pollinated by a highly diverse insect assemblage including species belonging to Diptera, Hymenoptera, Coleoptera and Lepidoptera orders (Herrera 1988; Żywiec et al., 2012; Authors, *unpublished data*). Inflorescences bear hermaphrodite flowers with radial symmetry and usually five oval petals. They have 3–20 (mean 9.5 ± 0.5) flowers per inflorescence, a petal length of 6.7–19.6 mm (mean ± 1SE = 12.0 ± 0.2 mm) and a petal area of 23.5–218.0 mm^2 (mean ± 1SE = 80.0 ± 2.8 mm^2). Mean corolla and calyx area is 417.2 ± 0.35 mm^2 and 30.7 ± 1.9 mm^2, respectively; and nectar per flower is 0–18.5 μL (mean ± 1SE = 2.0 ± 0.5 μL) (Żywiec et al., 2012). Flowers have five styles and 20–25 stamens (Aldasoro et al., 1996). Fruits are non-dehiscent globose pomes with 2–3 cm diameter and weight of ~9.5 g (Fedriani and Delibes 2009). Aborted fruits, smaller than ripe fruits, are a rounded dry, dark brown pome of small size (1–2 cm; Fedriani et al., 2020b). Each one includes usually 0–3 apparently developed seeds (25–50 mg each; Fedriani et al., 2020b) within very hard pericarps. The possibility of germination of these seeds of aborted fruits and contribute to recruitment, is often assumed to be nil (Fedriani et al., 2015; Castilla et al., 2019A; but see Fedriani et al., 2020b). Mature seeds are more than four times heavier than aborted seeds (Fedriani et al., 2018). Fruit production varies markedly among trees and years (Fedriani et al., 2015). Ripe fruits are dispersed mostly by Eurasian badgers *Meles meles* and red foxes *Vulpes vulpes* (Garrote et al., 2018; Fedriani et al., 2019, 2020a; Selwyn et al., 2020).

2.2. Tree size, flowering phenology and flower weight

We monitored daily the flowering phenological status of every georeferenced tree within the study plot for two consecutive years (N = 67 and 73 trees in 2019 and 2020, respectively). The monitoring covered a 27-day period between February and March in both studied years. Flowering phenological status of each tree was recorded early morning, regardless of the weather. No data was recorded for 2 days in 2019 and one day in 2020. We distinguished four pre-flowering stages involving different stages of flower bud development (Fig. 1): (a) flower buds are completely closed; (b) a small white tip is distinguished at the top of the flower bud; (c) inflorescences are visible and compact; and (d) inflorescence is unfolds, but flowers are still closed. One or two days after the inflorescence had unfolded, the first flowers opened and then, we recorded that day as "First flowering day". Since "First flowering day" was recorded, we also monitored four flowering phases based on the abundance of open flowers in the individual: 1) < 25% open flowers; 2) 25–50% open flowers; 3) 50–75% open flowers; and 4) > 75% open flowers (individual flowering peak). In 2019, three trees opened their
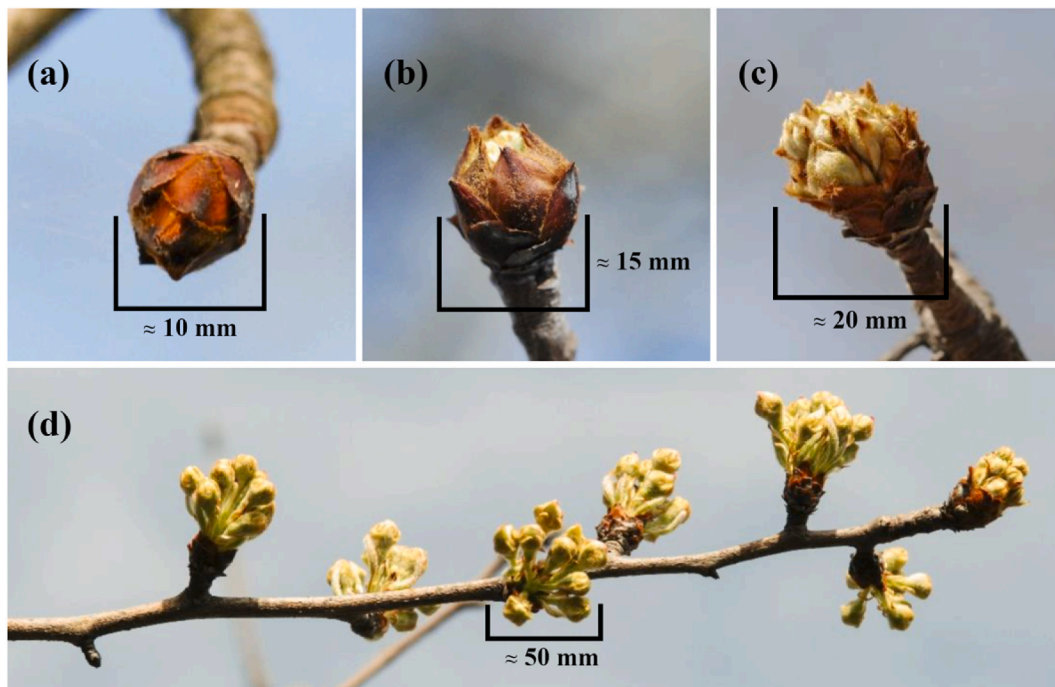
Fig. 1. Flower bud stages: flower buds are completely closed (a); small white tip is distinguished at the top (b); inflorescence buds are visible and compact (c); and inflorescence unfolds, but flowers are still closed (d).

first flowers before the beginning of field sampling, and seven trees that flowered in 2019, did not flower in 2020. To know the level of flowering synchrony among trees (spatiotemporal, not about differences in the intensity of the phenophase), we calculated the flowering synchrony index of Augspurger (1983) of each tree regarding the remaining ones in both study years (N = 66 in 2019 and 68 in 2020).

Flower weight is a measure that is related to flower size much easier to obtain than the actual flower size (Herrera 2020). Thus, during the peak of the flowering season, we collected around 20 flowers from each tree (14–29 and 5–28 flowers per tree in 2019 and 2020, respectively) well scattered in the tree crowns. We removed petioles with scissors and dried the flowers in a laboratory oven (J.P. SELECTA S.A.) at 65 °C during 1 h. Flower weight was measured with a PCE Instruments precision scale. We also characterized the tree size by measuring its diameter at breast height (DBH, hereafter).

2.3. Pollinator visitation

Pollination censuses were conducted during daytime since our previous observations and video records of flowering individuals indicate that insects visit flowers during daytime and not at nighttime (Authors *unpublished data*). We followed the sampling pollinator visitation method described in Herrera (2019). We conducted 3-min pollinator visitation, named "pollinator census" hereafter (i.e. basic sampling unit), in which we watched a flowering patch and counted its total number of open flowers. Censuses were done on lower and medium-upper canopy using a ladder, because canopy height can affect the irradiance received by flowering patches and potentially affect to the floral visitor community (Herrera 1995a). We recorded all pollinators visiting flowers in the patch during the 3-min period and the total number of flowers probed by each pollinator. We considered that pollinators "visit" a flower and therefore the patch, when they perch on the flower and touch the anthers with some part of their bodies.

Pollinator censuses were conducted in sunny and cloudy windless days from 10 a.m. to 5 p.m. The different flowering trees were monitored in random order of time and date pretending to have an hourly representation of each one. We used an area extent of approximately 1 m² to set our flower patches, adapted to assuredly of all pollinators' visitation at a distance of 1.5–2.0 m. We watched to approximately 22.61 ± 6.17 open flowers (6–56 open flowers) per patch. Sampled patches were randomly chosen at the moment of climbing the ladder. In total, we conducted 1,933 pollinator censuses on 67 trees and 46 different dates and accounting for a total watching effort of 5,799 flower·min^{-1}. We conducted 16.61 (4–45) censuses per individual (8.35 (2–22), and 8.38 (2–23) at lower and medium-upper canopy, respectively). In both years we sampled 26 days: from February 22nd to March 21st, in 2019; and from February 13th to March 12th in 2020. All censuses were conducted by a single observer, thus results have no bias from inter-observer heterogeneity.

2.4. Fruit production

In February–March, we randomly chose four branches in each tree within the study plot (N = 64) and we marked such branches with colored plastic tags. Due to unavailability of flowering branches, we used 1–3 branches in 16 trees. On each branch, we tagged four inflorescence buds using colored threads. During the flowering time, we counted the number of open flowers in each marked inflorescence; and then, in July, we counted the number of fruits borne by each marked infructescence. In 2019, just before the initiation of fruit fall in early September, we estimated the crop size of all reproductive trees within the study plot by counting their fruits (with binoculars when it was needed). Fruits are arranged in discrete clusters which facilitated estimation of reliable crop size by visually counting fruits from the ground (e.g. Fedriani et al., 2015).

2.5. Data analysis

We examined the effect of flowering synchrony (i.e. flowering synchrony index of Augspurger 1983), mean flower weight and spatial isolation to the ten nearest neighbors (nnd10, hereafter) on pollinator visitation using generalized linear mixed models (GLMMs). Flowering synchrony index was calculated using the function *SI2_onepop* executed in the R *flower* package (Wang 2015). First flowering day and flowering

synchrony exhibited a highly positive correlation leading to inflated collinearity in our models (VIF = 0.7), thus we discarded first flowering day in pollinator visitation and fruit production models. This was because the flowering synchrony index better accounts the expectation of a higher visitation rate and reproductive success in flowering synchronous individuals. We estimated the spatial isolation of each tree using the function *nndist* executed in the R *spatstat* package (Baddeley and Turner 2005). Specifically, we calculated the distance to the nearest neighbor (nnd1), to the five nearest neighbors (nnd5) and to the ten nearest neighbors (nnd10). We used two measurements of pollinator functional abundance as response variables: flower visitation probability and patch visitation probability (Herrera 2019). Flower visitation probability is defined as per-time-unit probability that one individual flower in the flowering patch was visited per census, estimated as the ratio of number of flowers visited to those available in the patch. Patch visitation probability is defined as per-time-unit probability that at least one pollinator entered to the flowering patch and probed at least one flower. Therefore, patch visitation probability was encoded as a binary variable with 1 and 0 whether the flowering patch was or not visited, respectively. We fitted GLMMs with binomial error distribution and logit link function using *glmer* implemented in the R *lme4* package (Bates et al., 2014). We included the total number of flowers in the flowering patch as a weight argument in models of flower visitation probability (Herrera 2019). In both analyses, we included year, tree and canopy nested within tree as random factors. We checked for overdispersion in our models using *dispersion_glmer* function from the R *blmeco* package (Korner-Nievergelt et al., 2015).

Fruit set is defined as the probability that flowers become developed fruits (Wesselingh 2007). Fruit set was analyzed fitting GLMMs with binomial error distribution and logit link function using *glmer* implemented in the R *lme4* package (Bates et al., 2014). We used as explanatory variables flowering synchrony, mean flower weight and nnd10. We also included DBH as an additional explanatory variable in our models, which is an estimate of tree size. We included the number of flowers of each inflorescence (tagged buds) as weight argument, and tree as random factor. We also check whether there was any relationship between the number of total visitations to the monitored flowers in each tree (total visitations within trees) and their fruit set. To do this, we fitted generalized linear models with binomial error distribution using *glm2* function from the R *glm2* package (Marschner 2011), setting fruit set as response variable and visitations as explanatory variable.

We used the same set of explanatory variables in the analysis of crop size (i.e. flowering synchrony, mean flower weight, nnd10 and DBH). We fitted GLMMs with Poisson error distribution using the function *glmer* implemented in the R *lme4* package (Bates et al., 2014). We included year, tree and canopy nested within tree as random factors. We detected twelve observations that behave as statistical outliers using the *romr.fnc* function from the R *LMERConvenienceFunctions* package (Tremblay 2013). The removal of these outliers did not affect the observed patterns. In those models in which we detected evidence of overdispersion, we included an observational-level random effect (Harrison 2014).

We used the Akaike Information Criterion (AIC) to compare models containing all possible combinations of the explanatory variables for each response variable analyzed, created with the *dredge* function from the R *MuMIn v1.43.17* package (Bartón 2020). Then, we tested whether the variables from selected models were significant based on Likelihood Ratio test with χ^2 distribution. Predicted means of our top-ranked models were obtained and plotted using the R *ggeffects* package (Lüdecke 2018). All analyses were performed in R 4.0.0 (R Core Team 2018).

3. Results

3.1. Pollinator visitation

For flower visitation probability, we found four top models with ΔAIC <2 (Table 1a). The distance to the ten nearest neighbors (nnd10) was the only explanatory variable in the top-ranked models showing a significant effect on flower visitation probability (Likelihood Ratio Tests: $\chi^2 = 23.70$, $P < 0.0001$). In other words, flowers of spatially isolated trees had greater flower visitation probability than those of spatially aggregated trees (Fig. 2a). Neither flower weight (LRT: $\chi^2 = 1.40$, $P = 0.24$; Fig. 2b) nor flowering synchrony (LRT: $\chi^2 = 0.80$, $P = 0.37$; Fig. 2c) had significant effects on flower visitation probability. Our results were consistent using mean distance to the nearest neighbor and to the five nearest neighbors (Table A1; Figs. A2 and A3).

Our results showed three models with ΔAIC <2 for patch visitation probability (Table 1b). Similarly to flower visitation probability, we found that only nnd10 had a significant effect on patch visitation probability (LRT: $\chi^2 = 17.21$, $P < 0.0001$). In other words, flowering patches of spatially isolated trees had a greater probability of being visited than those of spatially aggregated trees (Fig. 2d). Neither flower weight (LRT: $\chi^2 = 2.59$, $P = 0.11$; Fig. 2e) nor flowering synchrony (LRT: $\chi^2 = 0.001$, $P = 0.98$; Fig. 2f) showed a significant effect on the patch visitation probability. Our results were consistent using mean distance to the nearest neighbor and to the five nearest neighbors (Table A1; Figs. A2 and A3).

3.2. Fruit set

Four models had similar explanatory power on fruit set (Table 1c). We found that spatially aggregated trees had greater fruit set than spatially isolated trees (Fig. 3a), showing the spatial isolation a significant effect on fruit set (LRT: $\chi^2 = 13.59$, $P < 0.001$). Neither flower weight (LRT: $\chi^2 = 0.92$, $P = 0.35$; Fig. 3b), flowering synchrony (LRT: $\chi^2 = 0.98$, $P = 0.32$; Fig. 4a) nor the DBH (LRT: $\chi^2 = 0.10$, $P = 0.75$; Fig. 4b)

Table 1
Top-ranked models for pollinator visitation and reproductive success variables. Models are ranked based on the Akaike Information Criterion (AIC). Differences in AIC between each model and the model with lowest AIC (ΔAIC) are shown. Only models exhibiting ΔAIC <2 with the top model are shown for each response variable. For each model, Akaike's weights is indicated (ωi). *nnd10* means the distance to the ten nearest neighbors; *Flower weight*, the average weight of the trees' flowers; DBH, the diameter of the trunk at breast height; and *Synchrony*, the flowering synchrony index of the trees.

| Model statement	AIC	ΔAIC	ωi
Flower visit probability (a)			
nnd10	9760.70	0.00	0.367
nnd10 + Flower weight	9761.30	0.56	0.276
nnd10 + Synchrony	9761.90	1.16	0.205
nnd10 + Flower weight + Synchrony	9762.50	1.77	0.152
Patch visit probability (b)			
nnd10 + Flower weight	2208.20	0.00	0.418
nnd10	2208.70	0.59	0.312
nnd10 + Flower weight + Synchrony	2210.10	2	0.154
Fruit set (c)			
nnd10	1666.50	0.00	0.293
nnd10 + Synchrony	1667.50	1.01	0.177
nnd10 + Flower weight	1667.80	1.28	0.154
nnd10 + DBH	1668.70	1.96	0.11
Crop size (d)			
nnd10 + Flower weight + DBH	9063.40	0.00	0.293
nnd10 + Flower weight	9064.30	1.00	0.178
nnd10 + DBH	9064.70	1.40	0.146
nnd10 + Flower weight + Synchrony + DBH	9064.80	1.47	0.140
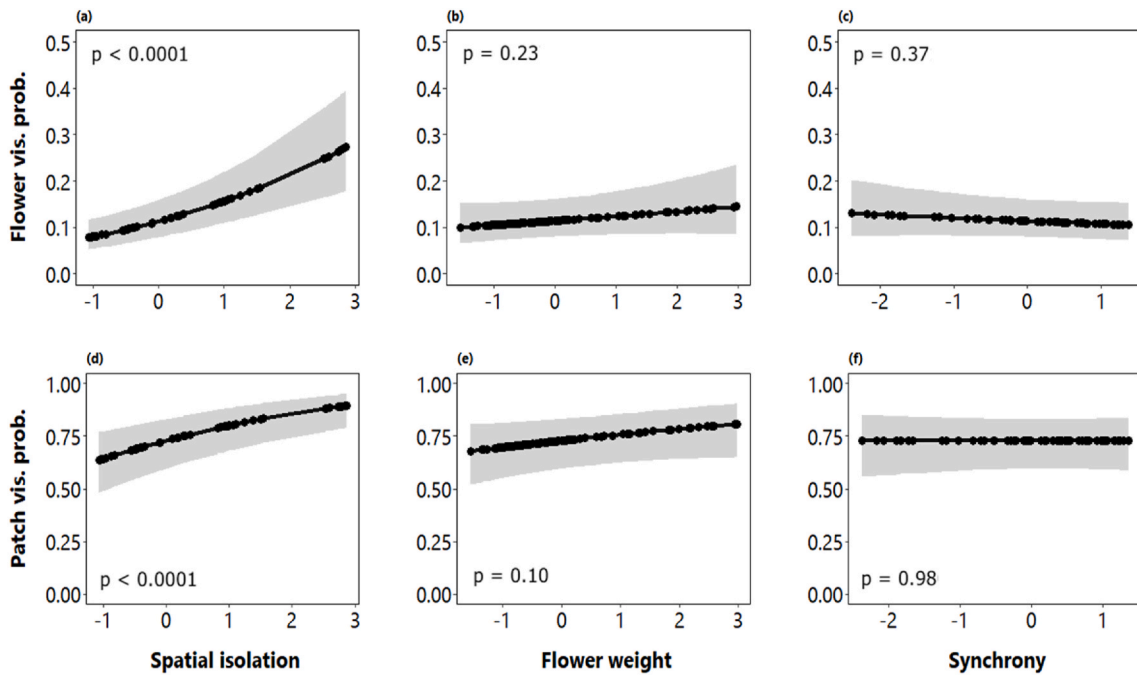
Fig. 2. Effects of tree spatial isolation, flower weight and flowering synchrony on pollinator visitation probability. The top panels showed the effect of our explanatory variables on flower visitation probability (i.e. per-time-unit probability that one individual flower in the flowering patch was visited per census), while the bottom panels showed the effects on patch visitation probability (i.e. per-time-unit probability that at least one pollinator entered to the flowering patch and probed at least one flower). Explanatory variables are standardized to mean zero and standard deviation one. Values of explanatory variables above and below zero indicate higher and lower spatial isolation (a, d), flower weight (b, e) or synchrony (c, f) than the population mean, respectively. The gray area shows 95% confidence intervals, and "p" indicates the p-value in Likelihood Ratio Tests.
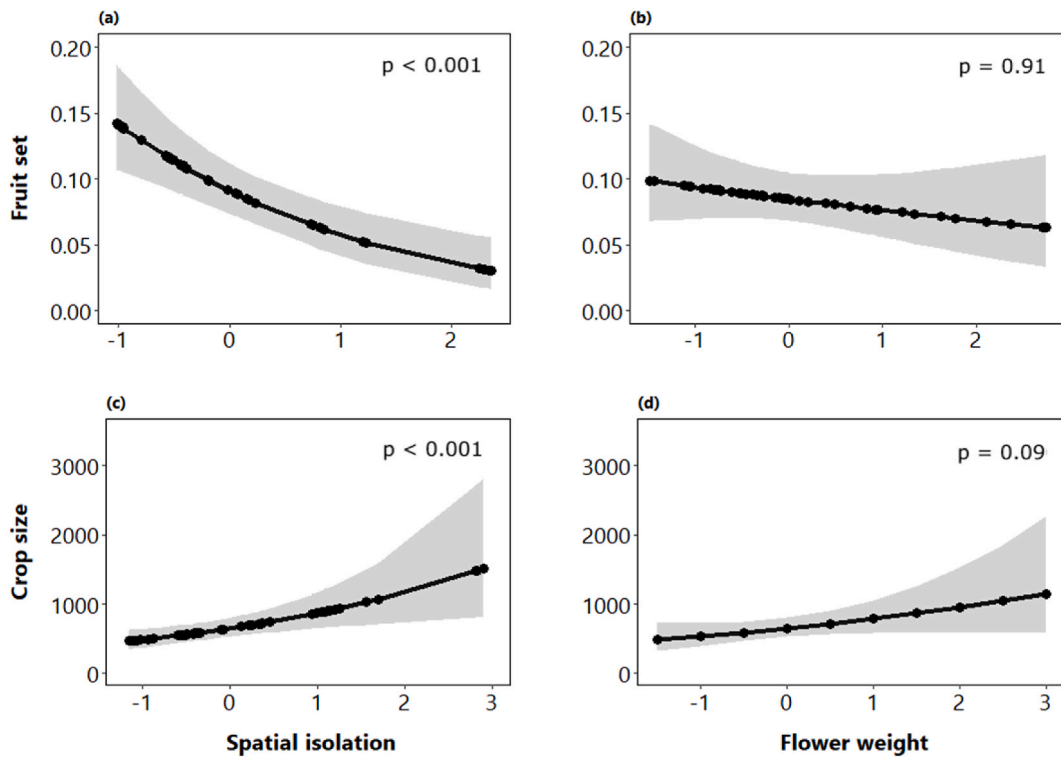

Fig. 3. Effects of tree spatial isolation and flower weight on reproductive success. The top panels showed the effect of our explanatory variables on fruit set (i.e. proportion of flowers setting fruits), while the bottom panels showed the effects on crop size (i.e. total fruit production per individual). Explanatory variables are standardized to mean zero and standard deviation one. Values of explanatory variables above or below zero indicate greater and lower spatial isolation (a, c) or flower weight (b, d) than the population mean, respectively. The gray area shows 95% confidence intervals, and "p" indicates the p-value in Likelihood Ratio Tests.
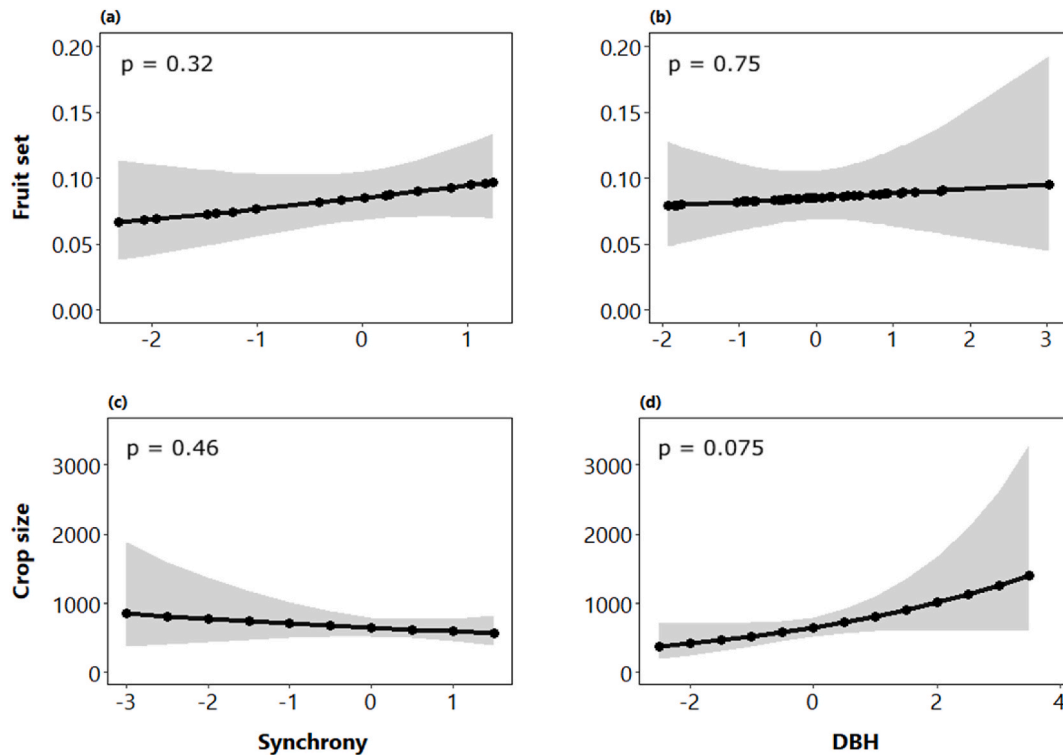
Fig. 4. Effects of tree flowering synchrony and DBH on reproductive success. The top panels showed the effect of our explanatory variables on fruit set (i.e. proportion of flowers setting fruits), while the bottom panels showed the effects on crop size (i.e. total fruit production per individual). Explanatory variables are standardized to mean zero and standard deviation one. Values of explanatory variables above or below zero indicate greater and lower flowering synchrony (a, c) or tree size (b, d) than the population mean, respectively. The gray area shows 95% confidence intervals, and "p" indicates the p-value in Likelihood Ratio Tests.

had significant effect on fruit set. Our results were consistent using mean distance to the nearest neighbor (LRT: $\chi^2 = 0.047$, $P = 0.83$) and to the five nearest neighbors (LRT: $\chi^2 = 3.87$, $P = 0.05$) (Table A2; Figs. A4 and A5). We did not find any relationship between pollinator visits and fruit set (LRT: $\chi^2 = 0.06$, $P = 0.80$).

3.3. Crop size

We found four models with similar explanatory power on tree crop size (Table 1d). The distance to the ten nearest neighbors had a significant effect on crop size (LRT: $\chi^2 = 8.04$, $P < 0.01$). Hence, spatially isolated trees had greater crop size than spatially aggregated trees (Fig. 3c). Our results also supported a marginal effect of DBH on crop size (LRT: $\chi^2 = 3.18$, $P = 0.074$), with crop size increasing as the width of the tree trunk increases (Fig. 4d). Finally, we did not detect any effect neither of flowering synchrony (LRT: $\chi^2 = 4.84$, $P = 0.47$; Fig. 4c) or of mean flower weight (LRT: $\chi^2 = 2.86$, $P = 0.09$; Fig. 3d) on tree crop size. Our results were consistent using mean distance to the nearest neighbor and to the five nearest neighbors (Table A2; Figs. A4 and A5).

4. Discussion

In this study, we examined the effects of distance to flowering conspecifics and intrinsic features of individuals such as flowering phenology, tree size and flower size on pollinator visitation rates and reproductive success in the insect-pollinated tree *Pyrus bourgaeana.* Our results highlight an important role of spatial isolation affecting all intrinsic features of trees. Although spatial isolation had a positive effect on pollinator visitation and crop size, it had a negative effect on fruit set, which suggests a decline of compatible conspecific pollen donors with spatial isolation for our target self-incompatible tree. Altogether, our results stress the relevance of individuals' spatial distribution for self-incompatible trees exhibiting low individuals' densities.

4.1. Spatial isolation

Increased pollinator visitation rates in dense flowering patches have been frequently reported in the literature (House 1992; Kunin 1993; Lamont et al., 1993; Law and Lean 1999; Dick et al., 2008). In contrast, our results revealed that trees more spatially isolated have higher probabilities for pollinator visitation than those which are in dense neighborhoods. This pattern was consistent for flower visitation probability and patch visitation probability. In the same line, recent studies have found a negative effect of plant conspecific density on pollinator visitation rates for other self-incompatible species (Wagenius and Lyon 2010; Hendrickson et al., 2018). For instance, Wagenius and Lyon (2010) reported greater pollinator visitation in spatially isolated *Echinacea angustifolia* plants. The positive relation between distance to conspecifics and pollinator visitation rates could be more frequent than expected, and especially for self-incompatible species. A potential explanatory mechanism for this unusual pattern could be an inflated intraspecific competition for pollinators (Zimmerman 1980). In particular, intraspecific competition between pollinators would cause a displacement to less visited foraging areas and thus, a decline of pollinator visitation rates in aggregated individuals (Kunin 1997; Mustajärvi et al., 2001; Fedriani et al., 2015; Żywiec et al., 2018). An alternative explanatory mechanism could be the microhabitat occupied by trees. For instance, isolated individuals located in more thermal environments (e.g. plot edges), are more favorable for pollination by ectothermic animals (i.e. insects; Beattie 1971; Herrera 1995b, 1997; Zamora 1999; see in Herrera 2020) or for pollinator nesting (i.e. areas with increased abundance of bare ground; Steffan-Dewenter et al., 2002).

An intriguing result of our work is the contrasting effects of distance to conspecific trees on fruit set (i.e. relative reproductive success) and crop size (i.e. absolute reproductive success). Specifically, we found that more spatially isolated trees had lower proportion of flowers setting fruits, as predicted. Reduced fruit set in trees with higher pollinator

visitation probabilities support pollen but not pollinator limitation in more spatially isolated individuals of our self-incompatible tree species. Indeed, Ison and Wagenius (2014) found similar results for the self-incompatible perennial herb *Echinacea angustifolia* and as they point out, this pattern could be more frequent than expected in self-incompatible species. One explanation could be a decline in the availability of compatible pollen donors in spatially isolated trees. This decline in pollen donors can have detrimental consequences for fruit production in self-incompatible species due to (i) inflated selfing due to geitonogamy (i.e. pollen deposition among flowers of the same individual; Somanathan and Borges 2001; Somanathan et al., 2004; Meekers and Honnay 2011) and (ii) increased biparental inbreeding if close neighbors are genetically related (Ison et al., 2018; Suarez-Gonzalez and Good, 2014; Fedriani et al., 2015; Castilla et al., 2019a). Furthermore, a non-exclusive mechanism could be related to the effectiveness of pollinators depositing pollen on stigmas (Gómez et al., 2010; Castilla et al., 2017; Valverde et al., 2019). An increased abundance of low-effective pollinator species visiting spatially isolated trees could account for reduced fruit set in those individuals. Ongoing studies examining the pollinator identity of our visits will help to elucidate whether this hypothesis is plausible for our study system.

Despite their reduced fruit set, and in contrast with our initial predictions (Fedriani et al., 2015), more spatially isolated individuals had greater crop sizes. We posit a possible explanatory mechanism for this compensation in fruit production. Trees in dense neighborhoods, showing higher fruit set, could have lower access to resources (e.g. limited space, higher intra-specific competition and less water, moisture and nutrients available; Fedriani et al., 2015) which lead them to allocate fewer resources to reproduction and thus to produce, on average, lower numbers of flowers. In other words, it is possible that isolated individuals, having this greater access to resources, could grow further and thus produce on average more flowers per individual than trees living in dense neighborhoods (Fuchs et al., 2003). Even with a low proportion of flowers setting fruits, large flower production could compensate total fruit production (Ollerton and Lack 1998; Castilla et al., 2011).

4.2. Flowering synchrony

Some works have reported positive synchrony effects on plant reproductive success (e.g. fruit set; Torres et al., 2002; Rodríguez-Pérez and Traveset 2016). On the contrary, there are works that show the opposite trend with higher flowering synchrony leading to lower reproductive success in plants (Ison et al., 2018). Our findings revealed no relation between the flowering synchrony and pollinator visitation rates, fruit set and crop size. These results could be attributed to the prolonged flowering period of *P. bourgaeana* trees regarding the entire population flowering period (mean flowering time = 13 days [2–27 days]). Therefore, most individuals within population flowered somewhat at the same time (mean flowering synchrony in the population was 0.76 ± 0.15, A3 Table). This would increase the chances of having a large number of donors. Accordingly to our results, Gómez (1993) found that pollinators of *Hormathophylla espinosa* did not show any preference for synchronous plants. Interestingly, Torres et al. (2002) found that the effect of first flowering date was much more relevant than the effects of flowering synchrony and flowering duration. However, we must note that first flowering day and flowering synchrony were positively correlated in our study (*correlation* = 0.70, $P < 0.0001$).

4.3. Flower weight and DBH

Finally, we analyzed the average flower weight and the effect of DBH. Contrary to our expectations (Endress 1994; Yan et al., 2016), results from this study did not support a meaningful effect of flower weight on pollinator visitation probabilities, which means that pollinators visited trees regardless of the flower weight. We assumed heavier

flowers would have greater levels of floral reward (i.e. nectar and pollen). However, previous studies have found different levels of variation in nectar and morphological traits among *P. bourgaeana* trees (Żywiec et al., 2012). Therefore, a positive correlation between flower weight and floral reward could be questionable and must be explicitly addressed in further studies. Furthermore, some studies have shown that pollinators can have a greater capacity to respond to floral displays (i.e. total flower production) than to floral weight or size (Harder and Barrett 1995; Ohashi and Yahara 2002; Mitchell et al., 2004; Makino and Sakai 2007). In this regard, we found that tree size had a marginally positive effect on crop size, which might suggest higher reproductive investment in trees with larger size and thus, greater floral displays. We measured DBH as an indirect estimate of floral display because it is expected that larger trees will have a greater flower display (Weiner and Thomas 1986; Herrera 1993; Ollerton and Lack 1998; Kato and Hiura 1999; Torres et al., 2002; Castilla et al., 2017). However, we must note that we could not perform a correlation between DBH and the number of flowers per individual since this last variable was not measured. Therefore, a direct link between tree size and floral display has not been addressed for the study species yet. Furthermore, previous studies have found evidence of population aging (Żywiec et al., 2018) and thus, a considerable portion of these large trees could be experiencing reproductive decay due to aging, preventing a clear positive relationship between floral display and tree size. Taken together, our results suggest that larger isolated trees could have more access to resources, which translates into slightly greater crop sizes.

5. Conclusions

Our analyses of a self-incompatible *Pyrus bourgaeana* population in Doñana National Park disclose that of all our evaluated variables examined, spatial isolation had the most striking effect on our response variables. In light of the current findings, spatial isolation may not be as detrimental to plants as we might think, since isolated individuals have the greatest absolute reproductive success despite their lowest relative reproductive success (i.e. success per flower). Our results also suggest pollen but not pollinator limitation in spatially isolated trees. Interestingly, this potential pollen limitation seemed compensated with greater flower production in these spatially isolated trees. Under this scenario of sexual reproduction mediated by pollinators, our findings accentuate the relevance of individuals' spatial distribution for self-incompatible trees.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2022.103866.

References

Aldasoro, J., Aedo, C., Muñoz-Garmendia, F., 1996. The genus *Pyrus* L (Rosaceae) in south-west Europe and north Africa. Bot. J. Linn. Soc. 121, 143–158.

Alonso, C., Herrera, C.M., Ashman, T.L., 2012. A piece of the puzzle: a method for comparing pollination quality and quantity across multiple species and reproductive events. New Phytol. 193, 532–542.

Augspurger, C.K., 1983. Phenology, flowering synchrony, and fruit set of six neotropical shrubs. Biotropica 15, 257.

Baddeley, A., Turner, R., 2005. Spatstat: an R package for analyzing spatial point patterns. J. Stat. Software 12, 1–42.

Bartón, K., 2020. MuMIn: Multi-Model Inference. R package version 1.43.17.

Bates, D., Maechler, M., Bolker, B., Walker S, 2014. lme4: Linear Mixed- Effects Models Using Eigen and S4. R Package Version 1.1-7.

Beattie, A.J., 1971. Itinerant pollinators in a forest. Madrono 21, 120–124.

Castilla, A.R., Alonso, C., Herrera, C.M., 2011. Exploring local borders of distribution in the shrub *Daphne laureola*: individual and populations traits. Acta Oecol. 37, 269–276.

Castilla, A.R., Pope, N., Jha, S., 2015. Positive density-dependent reproduction regulated by local kinship and size in an understorey tropical tree. Ann. Bot., mcv170

Castilla, A.R., Godoy, J.A., Delibes, M., Rodriguez-Prieto, A., Fedriani, J.M., 2019b. Microgeographic variation in recruitment under adult trees: arrival of new genotypes or perpetuation of the existing ones? Plant Biol. 21, 695–705.

Castilla, A.R., Pope, N.S., O'Connell, M., Rodriguez, M.F., Treviño, L., Santos, A., Jha, S., 2017. Adding landscape genetics and individual traits to the ecosystem function paradigm reveals the importance of species functional breadth. Proc. Natl. Acad. Sci. USA 114, 12761–12766.

Castilla, A.R., Garrote, P.J., Żywiec, M., Calvo, G., Suárez-Esteban, A., Delibes, M., Godoy, J.A., Picó, F.X., Fedriani, J.M., 2019a. Genetic rescue by distant trees mitigates qualitative pollen limitation imposed by fine-scale spatial genetic structure. Mol. Ecol. 28, 4363–4374.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9, 129–136.

Dick, C.W., Hardy, O.J., Jones, F.A., Petit, R.J., 2008. Spatial scales of pollen and seed-mediated gene flow in tropical rain forest trees. Trop. Plant Biol. 1, 20–33.

Dreisig, H., 1995. Ideal free distributions of nectar foraging bumblebees. Oikos 72, 161.

Endress, P.K., 1994. Floral structure and evolution of primitive angiosperms: recent advances. Plant Systemat. Evol. 192, 79–97.

Fedriani, J.M., Delibes, M., 2009. Seed dispersal in the Iberian pear Pyrus bourgaeana: a role for infrequent mutualists. Ecoscience 16, 311–321.

Fedriani, J.M., Wiegand, T., 2014. Hierarchical mechanisms of spatially contagious seed dispersal in complex seed-disperser networks. Ecology 95, 514–526.

Fedriani, J.M., Wiegand, T., Delibes, M., 2010. Spatial pattern of adult trees and the mammal-generated seed rain in the Iberian pear. Ecography 33, 545–555.

Fedriani, J.M., Ayllón, D., Wiegand, T., Grimm, V., 2020a. Intertwined effects of defaunation, increased tree mortality, and density compensation on seed dispersal. Ecography 43, 1352–1363.

Fedriani, J.M., Calvo, G., Delibes, M., Ayllón, D., Garrote, P.J., 2020b. The overlooked benefits of synzoochory: rodents rescue seeds from aborted fruits. Ecosphere 11, e03298.

Fedriani, J.M., Wiegand, T., Ayllón, D., Palomares, F., Suárez-Esteban, A., Grimm, V., 2018. Assisting seed dispersers to restore oldfields: an individual-based model of the interactions among badgers, foxes and Iberian pear. J. Appl. Ecol. 55, 600–611.

Fedriani, J.M., Garrote, P.J., Calvo, G., Delibes, M., Castilla, A.R., Żywiec, M., 2019. Combined effects of seed provenance, plant facilitation, and restoration site on revegetation success. J. Appl. Ecol. 56, 996–1006.

Fedriani, J.M., Wiegand, T., Calvo, G., Suárez-Esteban, A., Jácome-Flores, M., Żywiec, M., Delibes, M., 2015. Unravelling conflicting density and distance-dependent effects on plant reproduction using a spatially explicit approach. J. Ecol. 103, 1344–1353.

Forsyth, S.A., 2003. Density-dependent seed set in the Haleakala silversword: evidence for an Allee effect. Oecologia 136, 551–557.

Fuchs, E.J., Lobo, J.A., Quesada, M., 2003. Effects of forest fragmentation and flowering phenology on the reproductive success and mating patterns of the tropical dry forest tree *Pachira quinata*. Conserv. Biol. 17, 149–157.

Garrote, P.J., Calvo, G., Żywiec, M., Delibes, M., Suárez-Esteban, A., Fedriani, J.M., 2018. Strong among population variation in frugivory strength by functional diverse frugivores: a 'reciprocal translocation' experiment. Oecologia 187, 143–154.

Ghazoul, J., 2005. Pollen and seed dispersal among dispersed plants. Biol. Rev. 80, 413.

Giménez-Benavides, L., Escudero, A., Iriondo, J.M., 2007. Reproductive limits of a late-flowering high-mountain Mediterranean plant along an elevational climate gradient. New Phytol. 173, 367–382.

Gómez, J.M., 1993. Phenotypic selection on flowering synchrony in a high mountain plant, *Hormathophylla Spinosa* (Cruciferae). J. Ecol. 81, 605–613.

Gómez, J.M., Abdelaziz, M., Lorite, J., Muñoz-Pajares, A.J., Perfectti, F., 2010. Changes in pollinator fauna cause spatial variation in pollen limitation. J. Ecol. 98, 1243–1252.

Gunton, R.M., Kunin, W.E., 2009. Density-dependence at multiple scales in experimental and natural plant populations. J. Ecol. 97, 567–580.

Harder, L.D., Barrett, S.C.H., 1995. Mating cost of large floral displays in hermaphrodite plants. Nature 373, 512–515.

Harrison, X.A., 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2, e616.

Hendrickson, E.C., Thompson, P.G., Cruzan, M.B., 2018. Density-dependent pollination and germination in the patchy vernal pool species *Lasthenia californica*. Int. J. Plant Sci. 179, 583–591.

Herrera, J., 1988. Pollination relationships in southern Spanish Mediterranean shrublands. J. Ecol. 76, 274–287.

Herrera, C.M., 1992. Historical effects and sorting processes as explanations of contemporary ecological patterns: character syndromes in Mediterranean woody plants. Am. Nat. 140, 421–446.

Herrera, C.M., 1993. Selection on floral morphology and environmental determinants of fecundity in a hawk moth-pollinated violet. Ecol. Monogr. 63, 251–275.

Herrera, C.M., 1995a. Microclimate and individual variation in pollinators: flowering plants are more than their flowers. Ecology 76, 1516–1524.

Herrera, C.M., 1995b. Floral biology, microclimate, and pollination by ectothermic bees in an early-blooming herb. Ecology 76, 218–228.

Herrera, C.M., 1997. Thermal biology and foraging responses of insect pollinators to the forest floor irradiance mosaic. Oikos 78, 601–611.

Herrera, C.M., 2019. Complex long-term dynamics of pollinator abundance in undisturbed Mediterranean montane habitats over two decades. Ecol. Monogr. 89, e01338.

Herrera, C.M., 2020. Flower traits, habitat, and phylogeny as predictors of pollinator service: a plant community perspective. Ecol. Monogr. 90, e01402.

Hildesheim, L.S., Opedal, Ø.H., Armbruster, W.S., Pélabon, C., 2019. Fitness costs of delayed pollination in a mixed-mating plant. Ann. Bot. 124, 869–881.

House, S.M., 1992. Population density and fruit set in three dioecious tree species in Australian tropical rain forest. J. Ecol. 80, 57.

Inouye, B.D., Ehrlén, J., Underwood, N., 2018. Phenology as a process rather than an event: from individual reaction norms to community metrics. Ecol. Monogr. 89, e01352.

Ison, J., Wagenius, S., 2014. Both flowering time and distance to conspecific plants affect reproduction in *Echinacea angustifolia*, a common prairie perennial. J. Ecol. 102, 920–929.

Ison, J.L., Prescott, L.J., Nordstrom, S.W., Waananen, A., Wagenius, S., 2018. Pollinator-mediated mechanisms for increased reproductive success in early flowering plants. Oikos 127, 1657–1669.

Jha, S., Kremen, C., 2013. Resource diversity and landscape-level homogeneity drive native bee foraging. Proc. Natl. Acad. Sci. USA 110, 555–558.

Kacelnik, A., Krebs, J.R., Ens, B., 1986. Foraging in a changing environment: an experiment with starlings (*Sturnus vulgaris*). Quant. Analyses Behav. 6, 63–87.

Kato, E., Hiura, T., 1999. Fruit set in *Styrax obassia* (Styracaceae): the effect of light availability, display size, and local floral density. Am. J. Bot. 86, 495–501.

Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mitchell, R.J., Ashman, T.L., 2005. Pollen limitation of plant reproduction: pattern and process. Annu. Rev. Ecol. Evol. Syst. 36, 467–497.

Knudsen, J.T., Tollsten, L., 1993. Trends in floral scent chemistry in pollination syndromes: floral scent composition in moth-pollinated taxa. Bot. J. Linn. Soc. 113, 263–284.

Korner-Nievergelt, F., Roth, T., von Felten, S., Guelat, J., Almasi, B., Korner-Nievergelt, P., 2015. Bayesian Data Analysis in Ecology Using Linear Models with R, BUGS and Stan. Elsevier.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol. Lett. 10, 299–314.

Kunin, W.E., 1993. Sex and the single mustard: population density and pollinator behavior effects on seed-set. Ecology 74, 2145–2160.

Kunin, W.E., 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of Brassica kaber. J. Ecol. 85, 225–234.

Lamont, B.B., Klinkhamer, P.G.L., Witkowski, E.T.F., 1993. Population fragmentation may reduce fertility to zero in Banksia goodii – a demonstration of the Allee effect. Oecologia 94, 446–450.

Law, B.S., Lean, M., 1999. Common blossom bats (*Syconycteris australis*) as pollinators in fragmented Australian tropical rainforest. Biol. Conserv. 91, 201–212.

Lüdecke, D., 2018. Ggeffects: tidy data frames of marginal effects from regression models. J. Open Source Softw. 3, 772.

MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. Am. Nat. 100, 603–609.

Makino, T.T., Sakai, S., 2007. Experience changes pollinator responses to floral display size: from size-based to reward-based foraging. Funct. Ecol. 21, 854–863.

Marschner, I.C., 2011. glm2: fitting generalized linear models with convergence problems. The R J. 3, 12–15.

Meekers, T., Honnay, O., 2011. Effects of habitat fragmentation on the reproductive success of the nectar-producing orchid *Gymnadenia conopsea* and the nectar-less *Orchis mascula*. Plant Ecol. 212, 1791–1801.

Mitchell, R.J., Karron, J.D., Holmquist, K.G., Bell, J.M., 2004. The influence of *Mimulus ringens* floral display size on pollinator visitation patterns. Funct. Ecol. 18, 116–124.

Munguía-Rosas, M.A., Ollerton, J., Parra-Tabla, V., De-Nova, J.A., 2011. Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured: phenotypic selection on flowering phenology. Ecol. Lett. 14, 511–521.

Mustajärvi, K., Siikamäki, P., Rytkönen, S., Lammi, A., 2001. Consequences of plant population size and density for plant–pollinator interactions and plant performance. J. Ecol. 89, 80–87.

Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., et al., 2010. Plant phenotypic plasticity in a changing climate. Trends Plant Sci. 15, 684–692.

Ohashi, K., Yahara, T., 2002. Visit larger displays but probe proportionally fewer flowers: counterintuitive behaviour of nectar-collecting bumble bees achieves an ideal free distribution. Funct. Ecol. 16, 492–503.

Ollerton, J., Lack, A., 1998. Relationships between flowering phenology, plant size and reproductive success in shape *Lotus corniculatus* (Fabaceae). Plant Ecol. 139, 35–47.

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos 120, 321–326.

Paschke, M., Bernasconi, G., Schmid, B., 2005. Effects of inbreeding and pollen donor provenance and diversity on offspring performance under environmental stress in the rare plant *Cochlearia bavarica.* Basic Appl. Ecol. 6, 325–338.

Picó, F.X., Retana, J., 2000. Temporal variation in the female components of reproductive success over the extended flowering season of a Mediterranean perennial herb. Oikos 89, 485–492.

Pope, N.S., Jha, S., 2018. Seasonal food scarcity prompts long-distance foraging by a wild social bee. Am. Nat. 191, 45–57.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rodríguez-Pérez, J., Traveset, A., 2016. Effects of flowering phenology and synchrony on the reproductive success of a long-flowering shrub. AoB Plants plw007.

Sánchez, A.M., Albert, M.J., Rodríguez, M., Escudero, A., 2012. Extended flowering in a Mediterranean shrub: seasonal variability in seed quality and quantity. Flora 207, 821–827.

Selwyn, M., Garrote, P.J., Castilla, A.R., Fedriani, J.M., 2020. Interspecific interactions among functionally diverse frugivores and their outcomes for plant reproduction: a new approach based on camera-trap data and tailored null models. PLoS One 15, e0240614.

Somanathan, H., Borges, R.M., 2001. Nocturnal pollination by the carpenter bee *Xylocopa tenuiscapa* (Apidae) and the effect of floral display on fruit set in *Heterophragma quadriloculare.* Biotropica 33, 78–89.

Somanathan, H., Borges, R.M., Chakravarthy, V.S., 2004. Does neighborhood floral display matter? Fruit set in carpenter bee-pollinated *Heterophragma quadriloculare* and beetle-pollinated *Lasiosiphon eriocephalus.* Biotropica 36, 139–147.

Steffan-Dewenter, I., Münzenberg, U., Buerger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421–1432.

Suarez-Gonzalez, A., Good, S.V., 2014. Pollen limitation and reduced reproductive success are associated with local genetic effects in *Prunus virginiana*, a widely distributed self-incompatible shrub. Ann. Bot. 113, 595–605.

Torres, E., Iriondo, J.M., Pérez, C., 2002. Vulnerability and determinants of reproductive success in the narrow endemic *Antirrhinum microphyllum* (Scrophulariaceae). Am. J. Bot. 89, 1171–1179.

Traveset, A., 1995. Reproductive ecology of *Cneorum tricoccon* L. (Cneoraceae) in the Balearic Islands. Bot. J. Linn. Soc. 117, 221–232.

Tremblay, A., 2013. LMER Convenience Functions: a Suite of Functions to Back-Fit Fixed Effects and Forward-Fit Random Effects, as Well as Other Miscellaneous Functions, version 2.10.

Valverde, J., Perfectti, F., Gómez, J.M., 2019. Pollination effectiveness in a generalist plant: adding the genetic component. New Phytol. 223, 354–365.

Waites, A.R., Ågren, J., 2004. Pollinator visitation, stigmatic pollen loads and among-population variation in seed set in *Lythrum salicaria*. J. Ecol. 92, 512–526.

Wagenius, S., Lyon, S.P., 2010. Reproduction of *Echinacea angustifolia* in fragmented prairie is pollen-limited but not pollinator-limited. Ecology 91, 733–742.

Wang, X., 2015. Flower: Tools for Characterizing Flowering Traits. R Package Version 1.0.

Weiner, J., Thomas, S.C., 1986. Size variability and competition in plant monocultures. Oikos 47, 211.

Weiss, M.R., 2001. Vision and learning in some neglected pollinators: Beetles, flies, moths and butterflies. In: Chittka, L., Thomson, J. (Eds.), Cognitive Ecology of Pollination, pp. 171–190.

Wesselingh, R.A., 2007. Pollen limitation meets resource allocation: towards a comprehensive methodology. New Phytol. 174, 26–37.

Yan, J., Wang, G., Sui, Y., Wang, M., Zhang, L., 2016. Pollinator responses to floral colour change, nectar and scent promote reproductive fitness in *Quisqualis indica* (Combretaceae). Sci. Rep. 6, 24408.

Zamora, R., 1999. Conditional outcomes of interactions: the pollinator–prey conflict of an insectivorous plant. Ecology 80, 786–795.

Zimmerman, M., 1980. Reproduction in Polemonium: competition for pollinators. Ecology 61, 497–501.

Żywiec, M., Delibes, M., Fedriani, J.M., 2012. Microgeographical, inter-individual, and intra-individual variation in the flower characters of Iberian pear *Pyrus bourgaeana* (Rosaceae). Oecologia 169, 713–722.

Żywiec, M., Ledwoń, M., Holeksa, J., Seget, P., Łopata, B., Fedriani, J.M., 2018. Rare events of massive plant reproductive investment lead to long-term density-dependent reproductive success. J. Ecol. 106, 1307–1318.