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*Research article*

# Reproductive success, fruit removal and local distribution patterns in the early-flowering shrub *Daphne mezereum*

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In insect-pollinated, bird-dispersed plants, both investment in reproduction and reproductive success involve interactions between plants and their pollinators and dispersers. The outcome of these plant–animal interactions may be affected by the number of flowers and fruits, as well as by the plants' local environment and by spatial associations among plants. In this study we mapped the spatial distribution of individuals in a population of the early flowering, fleshy-fruited shrub *Daphne mezereum,* in a forest in boreo-nemoral Sweden. For all mapped individuals we collected data on numbers of flowers and fruits and fruit removal, for three consecutive years. We analysed spatial associations among individuals, and the effects on reproductive performance and fruit removal of plant height, numbers of flowers and fruits, distance to forest edge, and neighbouring flower and fruit density. Our results show that the density of *D. mezereum* increases with increasing proximity to forest edge. The number of flowers produced, as well as fruit set and fruit removal, show the same positive relationship with increasing proximity to forest edges. We further show that individuals are aggregated up to distances of about 10 m. The flower production of neighbouring conspecific individuals within 10 m is negatively related to fruit set whereas the fruit production of neighbours is positively related to fruit removal. Our main conclusion is that the spatial distribution of *D. mezereum* affects reproductive success and fruit removal, which in turn has the potential to feed back to the spatial distribution pattern. Combining studies of reproduction with spatial analyses is important to advance our understanding of the dynamics of plant populations.

Keywords: bird-dispersal, *Daphne mezereum*, density effects on reproduction, fruit removal, fruit set, hand pollination, insect-pollination, point-pattern analysis, spatial associations

## Introduction

The persistence of plant populations is dependent on successful reproduction of individual plants and the recruitment of new individuals. In insect-pollinated, bird-dispersed plants, these processes involve interactions between the plants and their pollinators and avian dispersers. The outcome of these plant–animal interactions, which

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determines the plant's reproductive success and its chances of being dispersed, is affected by the plant's surrounding environment.

The effects of a plant's surrounding environment, i.e. its environmental context, on reproduction and fruit removal depend on several factors. The position of an individual in the landscape, for example its distance to landscape features such as forest edges, may have both direct effects on the number of flowers and fruits produced, and indirect effects mediated by pollinators and dispersers on fruit set and fruit removal (Fig. 1a). Plants growing in different habitats will have different amounts of available resources to invest in reproduction, resulting in a variation in the number of flowers produced and on fruit set across the landscape. The number of flowers produced is directly related to the number of fruits or seeds produced, since the number of flowers and ovules produced sets a cap on the total reproductive success (Herrera 1991). The absolute number of fruits produced may in turn affect fruit removal rates, through effects of fruit crop on bird feeding behaviour (Jordano 1987, García et al. 2011, Albrecht et al. 2012). Moreover, the number of flowers produced may affect the fruit set or seed set, since pollinators can select plants based on the size of their inflorescences (Harder and Johnson 2009). The environmental context, such as distance to forest edges, also has the potential to affect pollination directly due to the pollinators' habitat preferences (Grundel et al. 2010). A plant's position in the landscape may also affect frugivorous birds directly, as their abundance can differ across habitats, with higher abundances at forest edges compared to forest interiors (Albrecht et al. 2013), which may affect fruit removal. Another aspect of the environmental context is the spatial associations among reproductive individuals (Fig. 1b). The spatial distribution of flowers within a population has the potential to affect pollinator behaviour (Fritz and Nilsson 1994, Goulson 2000) and the fruit crops of neighbouring plants have been found to positively affect both visitation rates and fruit removal rates, and to decrease dispersal distances (Carlo and Morales 2008, Guerra et al. 2017). Further, frugivorous birds tend to disperse seeds among fruit-bearing individuals, creating clustered patterns of vertebrate-dispersed plants (Jordano and Herrera 1995, García et al. 2005, Lázaro et al. 2005).

Taken together, this implies that the position relative to landscape elements and to other reproductive individuals has the potential to directly affect reproductive success, since available resources vary across habitats, and to indirectly affect fruit set and fruit removal through effects on pollinators and avian frugivores. These effects on fruit production and fruit removal thus both depend on and affect local distribution patterns (Fig. 1c).

*Daphne mezereum* is an early flowering, deciduous fleshy-fruited shrub native to the temperate parts of Europe (Hultén and Fries 1986). It is often found in semi-open habitats such as forest edges; has a generalized pollination system; and its fleshy fruits, which ripen in June and early July when few other vertebrate-dispersed plants have ripe fruits (Eriksson and Ehrlén 1991), are consumed by birds (Snow and Snow 1988).

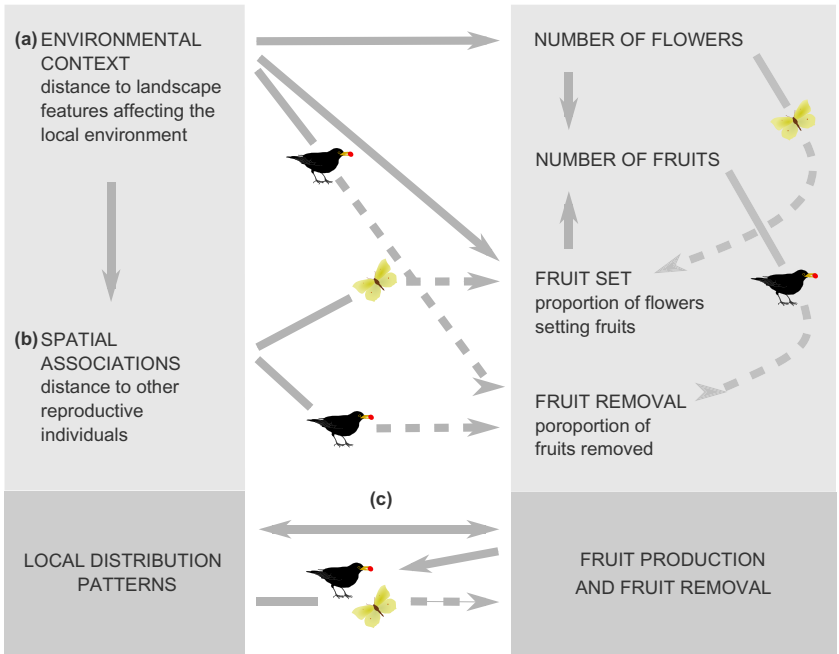



Figure 1. Potential direct and mediated effects of the surrounding environment of reproductive plants on reproductive success and fruit removal in insect-pollinated, bird-dispersed plants. (a) Direct and mediated effects of the environmental context. (b) Direct effects of spatial associations among reproductive individuals on pollinators and dispersers resulting in mediated effects on fruit set and fruit removal. (c) The surrounding environment of reproductive plants has the potential to affect fruit production and fruit removal. The production of fruits and the extent to which they are dispersed may feed back and affect local distribution patterns. Solid lines: direct effects. Dashed lines: effects mediated by pollinators and avian dispersers.

There exist very few studies on *D. mezereum* with a focus on reproduction (Manktelow 1991). However, for other *Daphne* species, plant traits and spatial location have been found to affect the reproductive success. Number of flowers has been reported to increase pollination and fruit set in *D. rodriguezii*, but not in *D. gnidium* (Rodríguez-Pérez and Traveset 2011). In *D. laureola*, the spatial location of plants affected the number of visiting beetles recorded, which were thought to be the main pollinator, with higher numbers in sunny locations (Alonso 2004). In *D. miyabeana*, fruit set was higher in open habitats compared to closed (Sakata and Nakahama 2018).

In the present study, we mapped a population of *D. mezereum* in south-eastern Sweden and estimated investment in reproduction and reproductive success for all individuals during three consecutive years. We also performed a pollination experiment to assess to what extent reproductive success in *D. mezereum* was limited by pollen availability. Our aim was to examine reproductive success and fruit removal in relation to plant traits, environmental context and spatial associations between reproducing individuals. *Daphne mezereum* flowers and sets fruit early, when the flowering and fruiting neighbourhood is composed almost exclusively of conspecific plants, which makes this species particularly interesting to study in this context. Our specific objectives were:

1) To describe the population characteristics with regard to size distribution, reproductive status, pollen limitation and spatial structure within the population and related to landscape features in the study area.
2) To examine whether number of flowers produced is related to plant size, distance to forest edge and flower production by neighbours. We predicted investment in reproduction to be positively related to plant size, with taller plants having more resources to invest in reproduction. Given the habitat preferences of *D. mezereum* in Sweden, we predicted investment in reproduction to be negatively related to the distance to forest edges.
3) To examine whether fruit set is affected by plant size, number of flowers per individual, distance to forest edge and the investment in reproduction of nearby conspecific individuals. Given the results from previous studies, we predicted relative reproductive success to be positively correlated with number of flowers in focal individuals. Given that generalist pollinators are expected to prefer sunny locations, such as forest edges, we also predicted a negative relationship between relative reproductive success and distance to forest edges. Given that more flowers in a patch often result in fewer visits per flower, we predicted fruit set to decrease with the number of nearby conspecific flowers.
4) To examine whether fruit removal is affected by plant size, number of fruits per individual (fruit crop), distance to forest edge and the fruit crop of nearby conspecific individuals. Given that fruit crop might increase fruit removal, we predicted the proportion of fruits that were removed to be positively related to number of fruits in focal individuals. Given that the fruiting neighbourhood can affect fruit removal, we also predicted fruit removal to increase with the size of the fruit crop of nearby conspecific individuals. Last, we predicted a negative relationship between fruit removal and distance to forest edges, given the expected increase in abundance of frugivorous birds in edge habitats.

## Material and methods

### Study species

*Daphne mezereum* is a deciduous shrub that can grow up to a height of 200 cm (Fig. 2a). The pinkish-purple, fragrant flowers appear before the leaves on the axis of the fallen leaves of the previous year (Tutin et al. 1964). In Sweden, *D. mezereum* is a relatively rare species found mainly on damp, humus-rich soils at forest edges or in deciduous forests previously managed as meadows or grazed by livestock (Swedish: 'lund') (Mossberg and Stenberg 2018). *Daphne mezereum* is one of the earliest species to flower in this region.

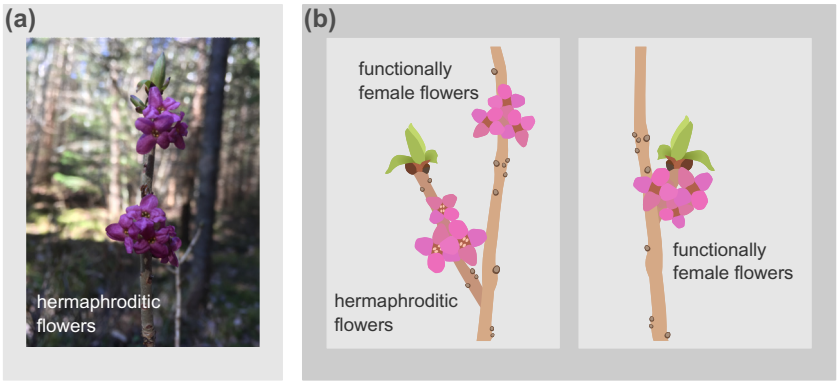



Figure 2. (a) *Daphne mezereum* at the study site in south-eastern Sweden. Four of the eight yellow anthers are visible in the centre of each hermaphroditic flower. (b) Illustration of the two sexual morphs found in this study and by Manktelow (1991). The majority of individuals had hermaphroditic and female flowers on the same individual. A small fraction of individuals had functionally female flowers only. The breeding system was thus a mix between gynomonoecy and gynodioecy.

Flowers are usually open from April to May, although during mild winters the onset of flowering can be as early as February (Lagerberg 1937). The fruits are fleshy, one-seeded drupes which turn from green to bright red at maturation. In Europe, the fruits are dispersed by birds such as the common blackbird *Turdus merula*, hazel grouse *Tetrastes bonasia*, European robin *Erithacus rubecula*, Eurasian blackcap *Sylvia atricapilla* and garden warbler *Sylvia borin* (Snow and Snow, 1988). The whole plant is poisonous to mammals (Cooper and Johnson 1984) and actively avoided by browsing ungulates (Suter et al. 2004, Boulanger et al. 2009). In Europe, *D. mezereum* seems to have a generalized pollination system and authors have reported visits by bombyliid flies, beetles, lepidopterans, aphids and parasitic wasps (Schultz, 1890, Kirchner 1911, Manktelow 1991). The details of the pollination system of *D. mezereum* in Sweden remains to be clarified (Manktelow 1991). Manktelow (1991) reported no visits by legitimate pollinators. Instead only smaller, mostly herbivorous insects were found inside the flowers. However, a bagging experiment showed that spontaneous self-pollination only resulted in a 10% fruit set compared to 67% when ambient pollination was allowed, which makes it likely that insect pollination resulting in cross-pollination or geitonogamy is commonly occurring. Further, Manktelow (1991) found that the study population included a large proportion of individuals with both functionally hermaphroditic and functionally female flowers, as well as a small proportion of individuals with only female flowers. Individuals in the population were thus gynomonoecious, i.e. having hermaphroditic and female flowers on the same individuals, or gynodioecious, i.e. having hermaphroditic flowers and female flowers on different individuals (Fig. 2b).

## Study site

This study was carried out on the peninsula of Väddö in the Stockholm archipelago in south-eastern Sweden (Fig. 3.). The study area covered approximately 4.8 ha, largely located in a forest, and was delimited to the west and south-east by linear openings in the forest, consisting of a power line corridor and a small gravel road, respectively. From hereon, these will be referred to as forest edges. In the area, the forest is dominated by Norway spruce *Picea abies*, with deciduous species (e.g. birch *Betula* spp. and aspen *Populus tremula*) occurring mostly in forest edges and in forest gaps. The field layer is dominated by mosses (e.g. gittering wood-moss *Hylocomium splendens* and red-stemmed feather-moss *Pleurozium schreberi*) and the dwarf shrub European blueberry *Vaccinium myrtillus*. Apart from *D. mezereum*, the understory layer consists mainly of sparsely distributed alpine currant *Ribes alpinum* and fly honeysuckle

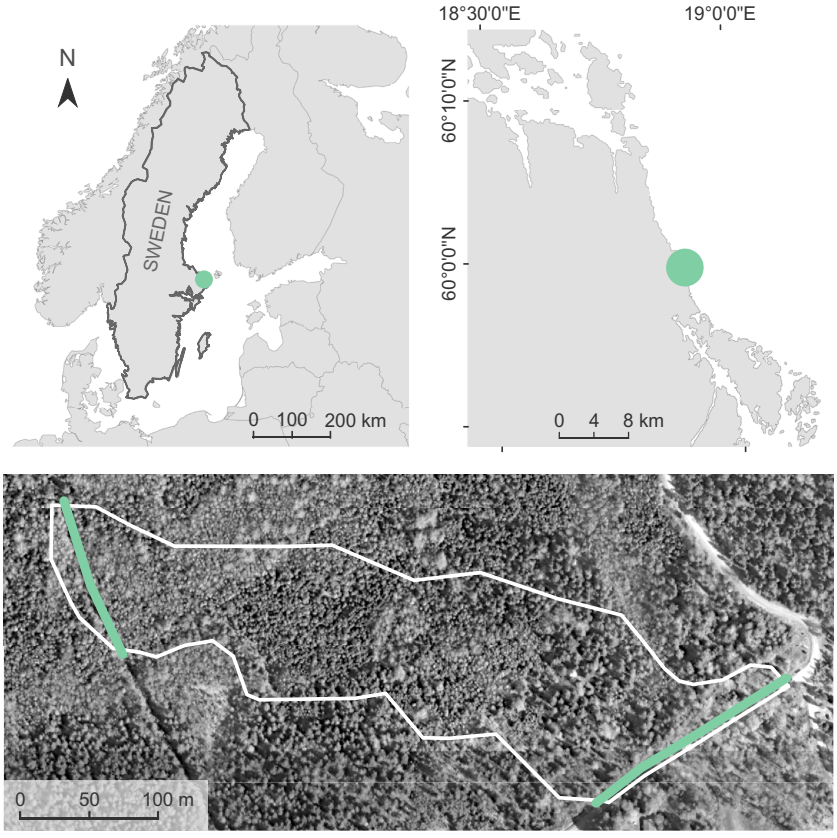



Figure 3. Maps of the study site and study area and their location in south-eastern Sweden and on the peninsula of Väddö in the Stockholm archipelago. Green dot: study site. White line: outline of the study population. Green lines: forest edges - to the west consisting of a power line corridor and to the southeast of a small gravel road.

*Lonicera xylosteum*. The soil consists of glacial till influenced by nearby occurring calcareous bedrock. The mean temperature for January is −3.5°C and the mean temperature for June is 15.9°C, with a mean annual precipitation of 595 mm.

## Field survey

During the years 2016–2018, we mapped all established individuals of *D. mezereum* of approximately 10 cm and higher within the study area. Individuals that were not detected during the first year were added continuously the following years of survey. In late April to early May we recorded the number of buds and flowers on each individual, as well as plant height. We recorded the number of fruits in June to August. During the first season it became apparent that many fruits disappeared soon after they ripened in July and that the later recordings thus underestimated reproductive success. The number of fruits used in the analyses thus correspond to the number of unripe green fruits recorded in June. In *D. kamtchatica*, most non-developing fruits were aborted within a week after flowers had wilted (Kikuzawa 1989), and so we believe that counting unripe fruits in June is an appropriate estimate of the reproductive success. The difference between number of fruits recorded in late summer (July–August) and the number of unripe fruits recorded in early summer (June) was used as an estimate of fruit removal.

### *Survey of flower gender and pollination experiment*

In 2019, to investigate if individuals were pollen limited, we surveyed 70 reproductive individuals. For each individual we recorded if flowers were hermaphroditic or female (anthers without pollen or lacking anthers). On individuals with more than one branch (n = 17), we performed a cross-pollination experiment. One branch was pollinated and the rest was left untreated as control. Pollen was taken from three or more randomly selected plants not included in the survey and applied with a small brush into each flower tube, on both hermaphroditic and female flowers. In April–May, we recorded the number of flowers and in June the number of developing fruits.

## Analyses

### *Size distribution and reproductive status*

To describe the size distribution of the population, and the relationship between size and reproductive status, we analysed the effect of height on reproductive status (vegetative versus reproductive) in all three survey years using a generalized linear model with a binomial error distribution in the 'stats' package in R (https://www.r-project.org/). To estimate the correlation between number of fruits and the number of flowers we calculated a Pearson's product moment correlation.

### *Pollination and fruit set*

To estimate the degree of pollen limitation, we compared fruit set between individuals having hermaphroditic flowers (producing pollen) and individuals having female flowers (producing no pollen), and assessed the effect of the pollen-addition treatment on fruit set. Data on flower gender were only available for individuals included in the pollination survey of 2019. However, data on fruit set for these individuals were available for three previous survey years. We thus analysed the effect of flower gender on fruit set for the individuals surveyed in 2019, using the data on fruit set from the three previous years, 2016–2018. Fruit set was defined as the proportion of flowers producing fruits. The difference in fruit set between individuals with hermaphroditic flowers and individuals with female flowers was analysed using a generalized linear mixed model with a binomial error distribution in the 'lme4' package (Bates et al. 2015), using the data from 2019. Fruit set was included in the model as successes (fruit) and failures (no fruit) of individual flowers, and the ID of each individual was included as a random effect.

We analysed the effect of pollination treatment on fruit set in individuals with both hand-pollinated and control branches (n = 17). Fruit set was included in the model as successes (fruit) and failures (no fruit). The effect of pollination treatment and flower genus (hermaphroditic/female) was analysed using a generalized linear mixed model with a binomial error distribution including the ID of each individual as a random effect.

### *Spatial associations*

To describe the spatial structure of the population, we estimated spatial associations among individuals of *D. mezereum* based on the spatial locations of all individuals in the three survey years (Fig. 4). Spatial associations were estimated using the inhomogeneous pair correlation function $g_{inhom}(r)$ (Baddeley et al. 2000) in the 'spatstat' package (Baddeley et al. 2015) in R (www.r-project.org). Spatial associations among individuals with the same reproductive status (reproductive/vegetative) were also estimated separately. We chose the inhomogeneous pair correlation function since some of the patterns displayed inhomogeneous densities (Baddeley et al. 2015), which is non-uniform intensity of points across the investigated area (Fig. 4). To estimate local densities included in all inhomogeneous pair correlation functions we used a Gaussian smoothing kernel with standard deviation $\sigma = 30$ m. We chose a value of standard deviation expected to exceed the scale of local clustering of individuals. Across our data set, the chosen standard deviation resulted in stable estimations of the pair correlation functions. We accounted for edge effects of unobserved points (occurrences of individuals outside the study site) by applying Ripley's isotropic correction and the translation correction (Ohser 1983, Ripley 1988, Baddeley et al. 2015). All pair correlation functions $g_{inhom}(r)$ were tested for deviations from a Poisson distribution using Monte Carlo simulation envelopes. We estimated 95% simulation envelopes based on 199 simulations of the null models selecting the fifth highest and fifth lowest values of $g_{inhom}(r)$ as the upper and lower bound of the envelopes.

To describe the spatial structure of the population in relation to landscape structures, we modelled the population density as a function of distance to forest edges. The analyses of spatial associations showed positive spatial associations

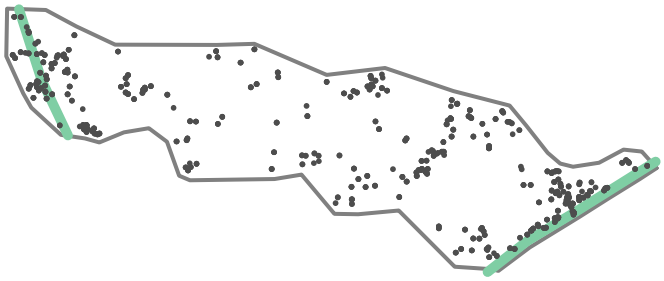


Figure 4. Spatial locations of individuals within the population of *Daphne mezereum* mapped in 2016–2018 in the study area in south-eastern Sweden. Green lines: forest edges.

between individuals within 10 m distance, which indicates clustering. This means that within 10 m of any individual, there are more other individuals than would be expected if all individuals were distributed randomly. We thus fitted an inhomogeneous cluster point process model to test the effect of distance to forest edge on the density of occurrences within the population. In other words, are there more individuals of *D. mezereum* close to forest edges (inhomogeneous distribution) than would be expected by chance, taking into account the clustered distribution pattern? We fitted an inhomogeneous Thomas cluster process (Stoyan and Stoyan 1994, Thomas 1994), which is widely used to model the intensity of plant distribution patterns (Wiegand et al. 2007, Jacquemyn et al. 2012, Quebbeman et al. 2021), with distance to forest edge (*distance to edge*) as a covariate. Edge effects of unobserved points were accounted for by applying Ripley's isotropic correction and the translation correction (Ohser 1983, Ripley 1988, Baddeley et al. 2015).

#### *Investment in reproduction, reproductive success and dispersal in relation plant traits and distribution patterns*

We considered six predictor variables when investigating the effects of plant traits and distribution patterns on number of flowers (investment in reproduction), fruit set (relative reproductive success) and fruit removal. The predictors included three traits: height, number of flowers and number of fruits; and three measures of spatial locations: distance to forest edge, total number of flowers within a 10 m radius (neighbouring flower density) and total number of fruits within a 10 m radius (neighbouring fruit density). We chose a radius of 10 m as the analyses of spatial associations showed positive spatial associations up to 10 m.

The effect of three variables (*height*, *distance to edge*, *neighbouring flower density*) on the number of flowers was analysed using a generalized linear model with a negative binomial error distribution using the 'MASS' package (Venables and Ripley 2002). In these models, *distance to edge* and *neighbouring flower density* can be seen as different measures of habitat suitability, with locations closer to forest edges and locations with high numbers of nearby flowers indicating suitable habitats. Since the effect of plant height on the production of flowers may vary with habitat suitability, our full models included interactions between *height* and *distance to edge* as well as *height* and *neighbouring flower density*. Model fit was evaluated by comparing AIC values between the full model and models including one or no interaction terms, choosing the model with the lowest AIC (Supporting information).

The effect of four variables (*height*, *flowers*, *distance to edge*, *neighbouring flower density*) on fruit set was analysed using a generalized linear mixed model with a binomial error distribution in the 'lme4' package (Bates et al. 2015) including the ID of each individual as a random effect to account for overdispersion. Since the effect of number of flowers on fruit set is mediated by pollinators and may vary with the plants' surrounding environment, our full models included interactions between *flowers* and *distance to edge* as well as *flowers* and *neighbouring flower density*. Model fit vas evaluated by comparing Akaike information criterion (AIC) values between the full model and models including one or no interaction terms, choosing the model with the lowest AIC (Supporting information). Fruit set was included in the model as successes (*fruit*) and failures (*no fruit*) of individual flowers.

The effect of four variables (*height*, *fruits*, *distance to edge*, *neighbouring fruit density*) on fruit removal was analysed using a generalized linear mixed model with a binomial error distribution in the 'lme4' package (Bates et al. 2015), including the ID of each individual as a random effect to account for overdispersion. Since the effect of number of fruits on fruit removal is mediated by dispersers and may vary with plant surrounding environment, our full models included interactions between *fruits* and *distance to edge*, as well as *fruits* and *neighbouring fruit density*. Model fit was evaluated by comparing AIC values between the full model and models including one or no interaction terms, choosing the model with the lowest AIC (Supporting information). Fruit removal was included in the model as successes (number of fruits removed) and failures (number of fruits not removed). In all models, because of the different scale of measurements, all variables were standardized by subtracting the mean and dividing them by their standard deviation. All statistical analyses were performed in R (www.r-project.org).

## Results

### Population characteristics

#### *Size distribution, reproductive status and pollen limitation*

In total, 322 individuals of *D. mezereum* were mapped during the three-year survey. Not all individuals were surveyed in all

years and new individuals were added continuously (Table 1). Height was associated with reproductive status, with reproductive individuals being taller than vegetative individuals (Supporting information). Individuals with female and hermaphroditic flowers had similar mean fruit set in all three survey years (Table 2). Flower gender did not affect fruit set in any of the survey years (Supporting information). For the untreated control individuals surveyed in 2019, the proportions of both fruit-bearing individuals and fruit set were much lower than in the previous years (Table 1). For the 17 individuals included in the pollination experiment, the hand-pollinated branches had a higher fruit set than the untreated branches (Table 3, Supporting information). As in the previous years, flower gender had no significant effect on fruit set (Supporting information).

#### *Spatial associations*

Individuals in the population were spatially clustered up to around 10 meters in all years (Fig. 5, Supporting information) and individuals with different reproductive status exhibited similar patterns of associations (2018: Fig. 5 and 2016–2018, Supporting information). The density of *D. mezereum* individuals decreased with distance to forest edges (2018: Fig. 5 and 2016–2018, Supporting information), taking into account their clustered distribution pattern. Overall density was lower for vegetative individuals than for reproductive individuals, resulting in a smaller decrease in density with distance to forest edge (2018: Fig. 5C and 2016–2018, Supporting information).

### Investment in reproduction, reproductive success and dispersal in relation to plant traits and distribution patterns

#### *Reproductive investment*

In all years, number of fruits was strongly correlated with number of flowers (Supporting information). The number of flowers was positively related to plant height in all three survey years (Fig. 6a–c, Supporting information). In 2016, we found an effect of the interaction between plant height and distance to forest edge (Fig. 6a). Close to forest edges, the number of flowers was only weakly related to plant height. With increasing distance to forest edges, the number of flowers was more strongly positively related to plant height. In 2017, the number of flowers was affected by the interaction between plant height and the number of flowers within a 10 m radius, the neighbourhood flower density (Fig. 6b). At locations with many flowers close by, the relationship between plant height and the number of flowers and fruits was negative.

The number of flowers was related to distance to forest edge in two out of three years (Fig. 6d–f, Supporting information). In 2016, the number of flowers decreased with distance to forest edge in short individuals, but increased with distance to forest edge in tall individuals (Fig. 6d). In 2017, the number of flowers and fruits decreased with distance to forest edge (Fig. 6e).

The number of flowers was positively related with the neighbouring flower density in all three years (Fig. 6g–I, Supporting information). However, in 2017 the number of fruits was positively related to neighbouring flower density only in short plants, but negatively related in tall plants (Fig. 6h).

#### *Relative reproductive success*

Fruit set was related to the number of flowers, distance to forest edge and the neighbouring flower density, but not related to height (Fig. 7, Supporting information). Fruit set was positively related to the number of flowers in all three survey years (Fig. 7d–f). In 2016, fruit set was negatively affected by distance to forest edge (Fig. 7g). In 2018, fruit set was negatively related to number of flowers within a 10 m radius, the neighbourhood flower density (Fig. 7l).

Table 1. Number of individuals surveyed, reproductive status, proportion of the flowering individuals producing fruits and mean fruit set of reproductive individuals. In 2019, only flowering individuals were surveyed. Proportions of fruit-bearing individuals and fruit set in 2019 are reported for the untreated control individuals (n = 41).

| | n | Flowering | Fruit bearing | Fruit set | |
|---|---|---|---|---|---|
| Surveys | | | | | |
| 2016 | 211 | 65% | 86% | 0.43 | ± 0.08 |
| 2017 | 264 | 56% | 81% | 0.33 | ± 0.06 |
| 2018 | 288 | 47% | 88% | 0.48 | ± 0.07 |
| Pollination survey | | | | | |
| 2019 | 70 | 100% | 24% | 0.08 | ± 0.03 |

Table 2. Number of individuals of the two flower genders and mean fruit set in 2016–2018. Data on flower gender of 70 individuals were recorded in 2019. Available data on fruit set presented for these individuals from the previous survey years. Significance: ***: < 0.001, **: < 0.01, *: < 0.05, .: < 0.1.

| Flower gender | n | Fruit set | |
|---|---|---|---|
| 2016 | | | |
| Female | 8 | 0.44 | ± 0.08 |
| Hermaphroditic | 34 | 0.43 | ± 0.06 |
| 2017 | | | |
| Female | 6 | 0.33 | ± 0.14 |
| Hermaphroditic | 35 | 0.35 | ± 0.03 |
| 2018 | | | |
| Female | 10 | 0.41 | ± 0.06 |
| Hermaphroditic | 43 | 0.56 | ± 0.05 |

Table 3. Treatments in the pollination experiment, number of individuals of the two flower genders and mean fruit set. In the pollination experiment only individuals with one hand-pollinated branch and one or more control branches with ambient pollination were included (n = 17). Significance: ***: < 0.001, **: < 0.01, *: < 0.05, .: < 0.1.

| Flower gender/treatment | n | Branch fruit set | |
|---|---|---|---|
| 2019 | | | |
| Female | 6 | 0.083 | ± 0.042 |
| Hermaphroditic | 28 | 0.105 | ± 0.056 |
| Ambient pollination | 17 | 0.019 | ± 0.004 |
| Hand-pollinated | 17 | 0.184 | ± 0.090** |

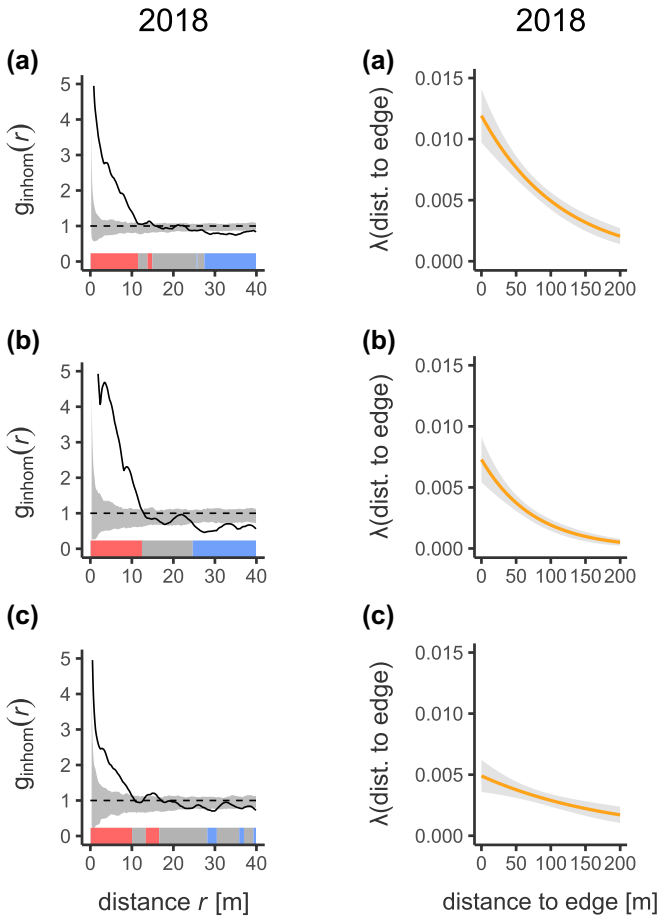



Figure 5. Spatial associations (left panel) and density as a function of distance to forest (right panel) for *Daphne mezereum* in 2018 for (a) all individuals, (b) reproductive individuals and (c) vegetative individuals. Left panel: Pair correlation function, $g_{inhom}(r)$, visualizing spatial associations of individuals. Red bars: spatial clustering indicated by values higher than one outside the simulation envelope (grey). Blue bars: spatial dispersion indicated by values lower than one outside the simulation envelope. Right panel: The fitted density of *D. mezereum* as a function of distance to forest edge (*distance to edge*) in 2018. Grey: pointwise 95% confidence interval.

### *Fruit removal*

Fruit removal was related to the number of fruits, distance to forest edge and the neighbouring fruit density but was not related to height (Fig. 8, Supporting information). In 2017, fruit removal was positively related to number of fruits and negatively related to distance to forest edge (Fig. 8e, h). In the two other years, fruit removal was affected by the interaction between the number of fruits and distance to forest edge (Fig. 8d, f, g–i). In plants with a low number of fruits, fruit removal was generally high and positively related to distance to forest edges. With increasing number of fruits, fruit removal was negatively related to distance to forest edge. In 2016 and 2018 we found a trend towards a positive relationship between fruit removal and the number of fruits within a 10 m radius, the neighbouring fruit density (Fig. 8l).

## Discussion

In this study, we found that reproduction and fruit removal in *D. mezereum* were influenced by plant traits as well as by environmental context and spatial associations of individual plants. Local distribution patterns revealed individuals to be aggregated in clusters of about 10 m with higher densities of individuals close to forest edges. By describing the population characteristics, we can assess how the observed variation in reproductive success and fruit removal has the potential to reinforce both the locally aggregated distribution pattern and the density patterns.

As predicted, we found a positive effect of plant size on investments in reproduction. Size may be seen as a measure of plant resource state reflecting the habitat quality, with suitable habitats promoting taller plants with more resources to invest in reproduction. In Sweden, forest edges are considered suitable habitats for *D. mezereum* (Jonsell 2010, Mossberg and Stenberg 2018). This was reflected by the higher densities of *D. mezereum* close to forest edges at our study site as well as by the decrease in reproductive investment with distance to forest edge. We further found a positive relationship between reproductive investment and the investment in reproduction of nearby conspecific individuals, indicating that reproductive investment depends on spatially autocorrelated environmental factors. This patchiness of suitable habitats may be a source of plant clustering. However, in perennial plants like *D. mezereum*, size is often correlated with plant age, with taller individuals also being older. This would weaken the predicted relationship between habitat quality and plant height, and may explain the contradictive result of positive effects of distance to forest edge on number of flowers, as well as the negative effect of neighbouring flower density in tall individuals. This was likely driven by a few tall, and possibly old, individuals with large number of flowers in the forest interior with few other flowering individuals nearby. The two measures of suitable habitat, distance to forest edge and neighbouring flower density, did not explain the reproductive success of these individuals.

The investment in flower production *D. mezereum* did had a positive effect on fruit set, with larger floral displays resulting in higher fruit set. In *D. rodriguezii*, flower production had a positive effect on fruit set, while no flower trait was found to affect fruit set in *D. gnidum* (Rodríguez-Pérez and Traveset 2011). Plants with large floral displays are often visited more frequently by pollinators than plants with smaller displays, and might have higher visitation rates per flower (Ohashi and Yahara, 1999), which may explain the positive relationship between number of flowers per individual and fruit set. However, in one of the survey years, fruit set decreased with the flower production of nearby individuals. This may indicate a dilution effect (Goulson 2000) where pollinators visit a smaller proportion of the available flowers in larger clusters of flowering individuals of *D. mezereum*. We also found a negative effect of distance to forest edge on fruit set in one of the survey years. Higher fruit set at forest edges may be attributed to increased resources available to

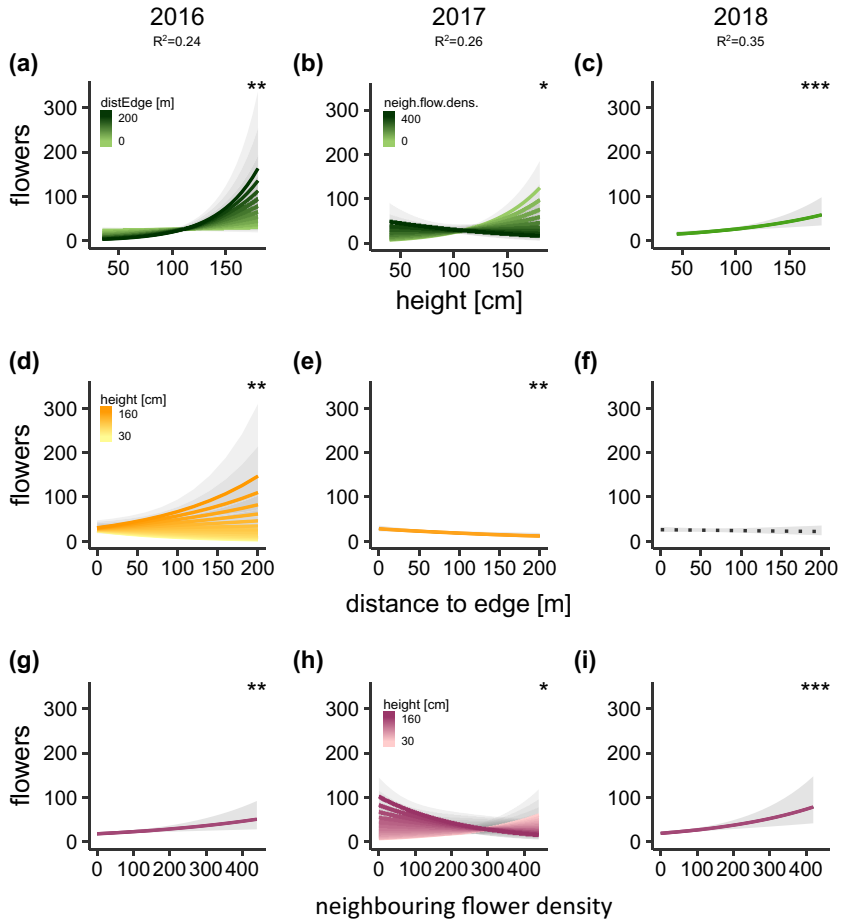



Figure 6. The number of flowers (*flowers*) in relation to plant height (a–c), distance to forest edge (*distance to edge*) (d–f) and the number of flowers of all individuals within a 10 m radius surrounding each individual (*neighbouring flower density*) (g–i) in 2016–2018. Solid lines represent significant relationships and trends ($p < 0.1$). Dotted lines represent non-significant relationships. $R^2$: variance explained by the model. Significance: ***: < 0.001, **: < 0.01, *: < 0.05, .: < 0.1.

invest in fruit maturation or to increased pollinator services (Montgomery et al. 2003). Although the effect of resource availability on fruit set in *D. mezereum* should be further investigated, this result – together with the evidence of pollen limitation – is in line with the effect of habitat on pollinators in the related species *D. laureola* and *D. miyabeana* (Alonso 2004, Sakata and Nakahama 2018). Taken together, our results suggests that the reproductive success of *D. mezereum* is, to some extent, mediated by legitimate pollinators and can vary across floral neighbourhoods and habitats.

We found only a weak positive effect of fruiting neighbourhood on fruit removal. In two of the years, the positive effect of plant fruit crop on fruit removal was only found for plants close to the forest edges. At larger distances to forest edges, fruit removal decreased with the number of fruits produced. This may have been due to a difference in the assemblage and abundance of birds consuming the fruits of *D. mezereum* between the edge and the forest habitat. The abundance of frugivorous birds has been found to be higher at forest edges compared to forest interiors, due to an increase in habitat generalists (Albrecht et al. 2013). This higher abundance might lead to an increase in consumers relative to fruit availability. If forest habitat specialists are less dependent on fruits in their diets, eat fruits only occasionally and do not actively search for fruits based on crop size, this would result in a decreasing proportion of fruits removed with increasing fruit crop and distance to forest edges.

The finding that *D. mezereum* reaches higher densities at forest edges is in line with the species habitat preferences (Mossberg and Stenberg 2018), and with previous findings of distribution patterns of fleshy-fruited species accumulating at the edges of open habitats (Arnell et al. 2019). The detailed mapping of plant individuals in combination with measures of reproductive success and fruit removal allows us to understand in some more detail how these local distribution patterns may have been shaped. In *D. mezereum* there seems to be a spatial concordance (sensu Schupp 1995) between different phases of the early regeneration process, in the sense that the spatial variables studied affected investment, reproductive success and fruit removal in the same direction in almost all cases. We show that individuals of *D. mezereum* produce more flowers and fruits at forest edges, leading to

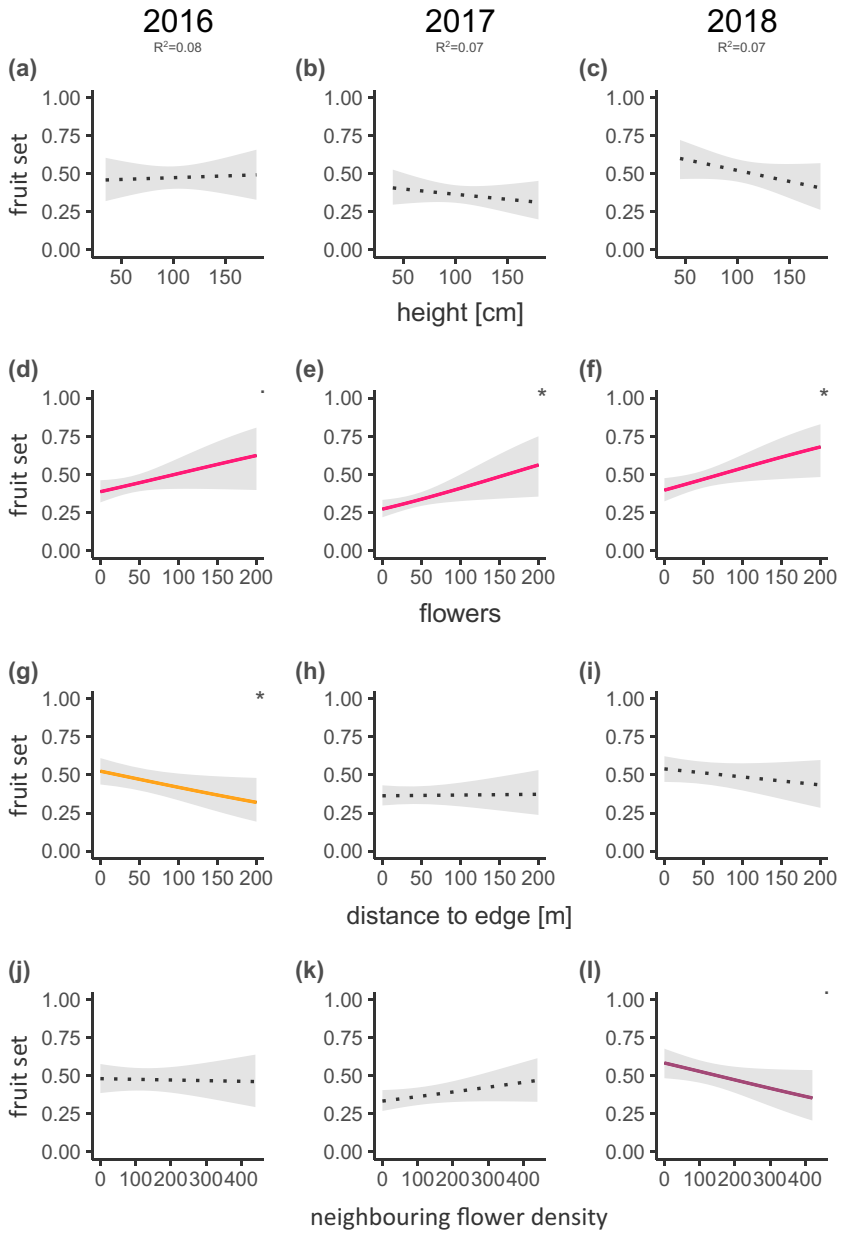



Figure 7. The relative reproductive success (*fruit set*) in relation to plant height (a–c), number of flowers (d–f), distance to forest edge (*distance to edge*) (g–i) and the number of flowers of all individuals within a 10 m radius surrounding each individual (*neighbouring flower density*) (j–l) in 2016–2018. Solid lines represent significant relationships and trends ($p < 0.1$). Dotted lines represent non-significant relationships. $R^2$: variance explained by the model. Significance: ***: < 0.001, **: < 0.01, *: < 0.05, .: < 0.1.

a relatively high abundance of seeds in this habitat, which should contribute to the accumulation of individuals. A high number of flowers also positively affected the pollination rate, measured as fruit set. Fruit set was found to be higher at forest edges, indicating that pollination is more effective in this habitat, although variable between years. The number of fruits produced in turn has positive effects on the proportion of fruits removed in edge habitats. The increased population density with decreasing distance to forest edges may thus be explained jointly by effects of edge habitats on investment in reproduction, and reproductive success mediated by pollination and fruit removal.

The small-scale clustering of individuals found in this study has also been found for other species of fleshy-fruited trees and shrubs in south-eastern Sweden (Arnell et al. 2021). The mechanisms behind this local distribution pattern are more difficult to resolve, given our results. Clustered patterns of vertebrate-dispersed plants may be the result of dispersal patterns (Jordano and Herrera 1995, García et al. 2005, Lázaro et al. 2005, Arnell et al. 2021) or simply the result of small-scale patchiness of suitable habitats. We found the investment in reproduction and the absolute reproductive success in *D. mezereum* to be positively related to the investment in reproduction of nearby conspecific individuals,

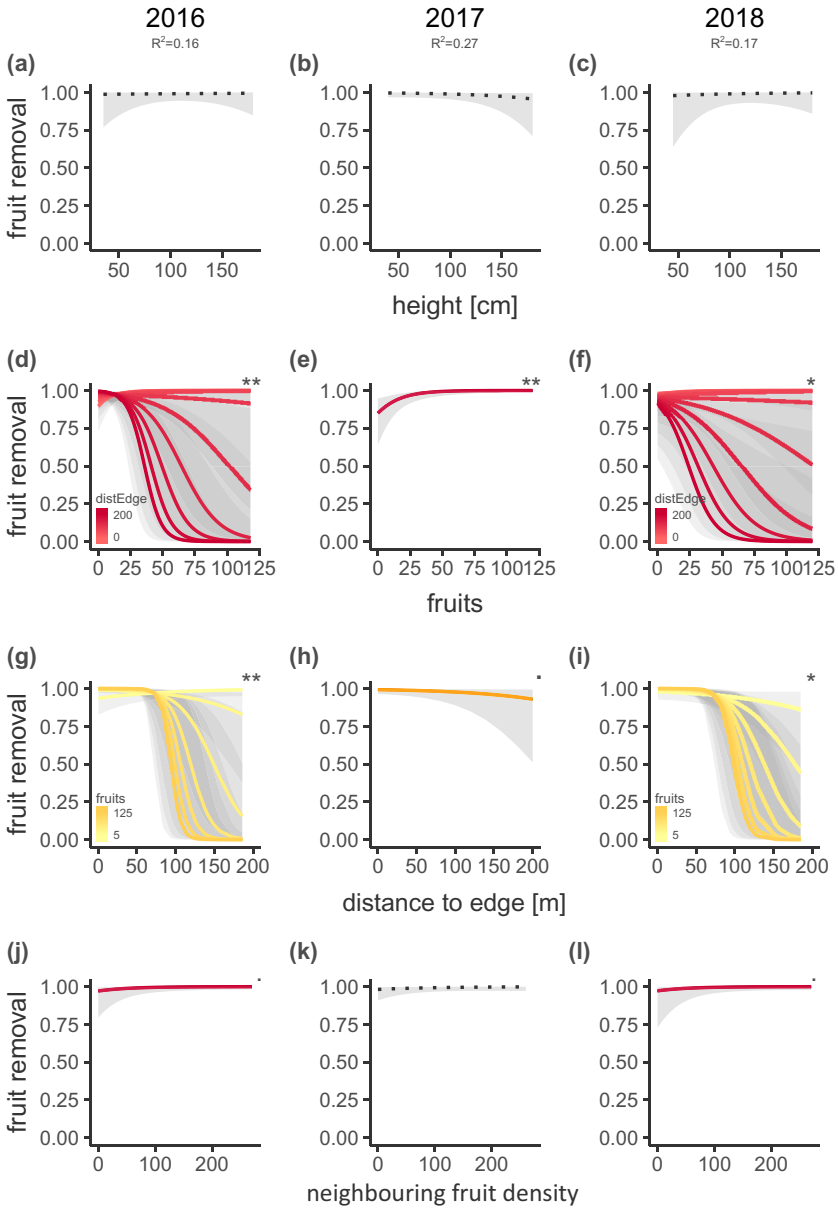



Figure 8. Proportion of fruits removed (*fruit removal*) in relation to plant height (a–c), number of fruits (d–f), distance to forest edge (*distance to edge*) (g–i) and the number of fruits of all individuals within a 10 m radius surrounding each individual (*neighbouring fruit density*) (j–l) in 2016–2018. Solid lines represent significant relationships and trends ($p < 0.1$). Dotted lines represent non-significant relationships. $R^2$: variance explained by the model. Significance: ***: <0.001, **: <0.01, *: <0.05, .: < 0.1.

indicating that patches of suitable habitats may affect the clustering of regenerating plants. However, since *D. mezereum* sets fruits early in the season when few other species bear fruits, our finding that more fruits are removed in patches with high numbers of conspecific fruits speaks in favour of birds promoting the clustered pattern. When the fruiting neighbourhood is composed almost exclusively of conspecific individuals, frugivorous birds are likely to disperse seeds among individuals of *D. mezereum*, creating or reinforcing clustered patterns. Irrespective of what mechanisms caused the pattern, the clustering of reproductive individuals resulted in both spatial concordance and discordance of regeneration processes, since the number of flowers of nearby reproductive individuals negatively affected the relative reproductive success. This may be due to a reduction in the number of pollinator visits with increased clustering of flowering individuals (Goulson 2000).

Plant spatial distributions depend on successful reproduction and recruitment. This study makes clear that spatial distribution also feeds back and affects reproductive success and fruit removal. In a broader perspective, our study illustrates that combining studies of reproduction with spatial analyses is a productive way to further our understanding of the dynamics of plant populations.

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### Author contributions

**Matilda Arnell**: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Ove Eriksson**: Conceptualization (equal); Methodology (equal); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Johan Ehrlén**: Conceptualization (equal); Methodology (equal); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

### Data availability statement

R-scripts and data to perform the analyses are available from the Figshare Digital Repository: https://doi.org/10.17045/sthlmuni.21311154. (Arnell et al. 2023).

### Supporting information

The Supporting information associated with this article is available with the online version.

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