Article

SPATIAL OCCUPANCY PATTERNS OF THE NURSERY POLLINATOR *DERELOMUS CHAMAEROPIS* AT ITS HOST PLANT, *CHAMAEROPS HUMILIS* (ARECACEAE)

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Abstract—Pollination success is influenced by factors such as density and distance from neighbouring conspecifics. However, the pure neighbourhood effects of spatial patterns of interaction on pollination success remains poorly understood. In this study, we used techniques of spatial point pattern analysis (SPPA) to investigate the relationship between the spatial distribution of a specialist pollinator, the weevil *Derelomus chamaeropis*, and the fruiting success of its host plant, the dwarf palm *Chamaerops humilis*, within a nursery pollination system. We georeferenced a dwarf palm population in a 22-hectare plot (96 individuals: 41 females/ 55 males), located at the Doñana National Park (SW Spain). We quantified the abundance and spatial pattern of adult weevil occupancy, and their correlation with the spatial distribution of dwarf palms. Additionally, we analysed the spatial pattern of fruiting success and how palm traits (number of inflorescences and flowers, and sex) influenced adult weevil abundance and fruiting success. Our findings revealed that presence/abundance of *D. chamaeropis* depended on plant sex, with female inflorescences showing significantly higher adult weevil abundances. We found a significant, negative density-dependent response, where higher neighbourhood density of palms led to reduced local weevil abundance. In contrast, we observed positive density and distance dependence for fruiting success at small spatial scales (2-5 m and 5-15 m), suggesting enhanced pollination success in dense patches. Our results indicate that weevil distribution is shaped by local resource availability and competitive interactions rather than broader palm arrangement. Additionally, pollination efficiency and fruit set benefit from positive distance-density dependence in dense patches.

Keywords—Insect pollination, weevil, fruiting success, palms, point pattern analysis, specialized pollination system, random patterns

INTRODUCTION

Population attributes, particularly the spatial distribution of individuals, can have a significant impact on pollination success in insect-pollinated plants. Among the extrinsic factors influencing pollination success, plant density (number of individuals per unit area) (Mustajärvi et al. 2001; Spigler & Chang 2009), spatial aggregation (Wiegand et al. 2007; Fedriani et al. 2015; Rodríguez-Rodríguez et al. 2015) and pollinator abundance (Aizen & Harder 2007; Hallett et al. 2017) have been highlighted in previous research. Various processes, such as biodiversity loss

(Vamosi et al. 2006), habitat fragmentation (Fahrig 2003), and land-use changes (Gallant et al. 2014; Moser et al. 2015) can disrupt plant-pollinator interactions (Harris & Johnson 2004; Bailey et al. 2010; Abramson et al. 2011). In remnant habitat fragments, changes in the pollinator community can lead to reduced visitation by pollinators, resulting in decreased reproductive output for plant species (Xiao et al. 2016). The loss of plant-pollinator interactions may trigger far-reaching, cascading changes in natural communities (Jordano 2016), leading to a loss of ecological functions (Valiente-Banuet et al. 2015).

The vulnerability of plants with highly specialized interactions with their pollinators to functional losses of their pollination service has been well documented (Johnson & Steiner 2000). These specialized pollination systems involve a few pollinator species that are efficient in pollinating plant species, and the interaction partners have tightly co-adapted life cycles that reciprocally depend on each other for reproduction (Johnson et al. 2012; Dufaÿ & Anstett 2003). The main threats of these systems are anthropogenic modifications to the local landscape (Klank et al. 2010; Geerts & Pauw 2012; Phillips et al. 2015) and climate change (Weaver & Mallinger 2022; Schweiger et al. 2010) that can directly affect the plant and the pollinator leading to a decrease in plant fitness and population density. The specificity of these interactions highlights the importance of their conservation due to the high risk of extinction or, ultimately, co-extinction (Johnson & Steiner 2000).

The visitation rate of insect pollinators in local plant patches can be influenced by the density and spatial aggregation of individuals, as these factors can affect the availability and accessibility of floral resources (Wiegand et al. 2006; Raventós et al. 2010; Fedriani et al. 2015). High-density patches may attract more pollinators due to positive, density-dependent responses to clumped resource abundance and reduced travel time among multiple patches (Jump & Peñuelas 2006; Fedriani et al. 2015). However, high-density populations can also experience competition for pollinator visits and resources, which may negatively impact fruit initiation and development (Gunton & Kunin 2009; Spigler & Chang 2009; Alonso-López et al. 2022).

Although these effects are generally expected, they can vary among pollinator species depending on their ecology and foraging behaviour (Hegland & Boeke 2006). Generalist pollinators often exhibit aggregative responses (Fontaine et al. 2008), whereas some specialist pollinators can locate isolated plants even in low-density situations (Nason et al. 1998; Franz 2007) due to coevolved response mechanisms (e.g., species-specific attractants and sensory abilities; Hossaert-McKey et al. 2010). The presence and abundance of pollinators can also depend on important intrinsic traits such as flowering synchrony (Jácome-Flores et al. 2018) and the number of flowers per plant (Augspurger 1981; Melampy 1987), which may affect intraspecific competition and dilution of pollinator visits (Fritz & Nilsson 1994; Larson & Barrett 2000; Delmas et al. 2014; Jácome-Flores et al. 2018). While highly specialized pollination systems are often vulnerable to environmental disturbances due to their reliance on specific pollinator species (Johnson & Steiner 2000), certain mechanisms may provide resilience even in highly modified landscapes. For instance, some pollinators exhibit behavioural plasticity, adjusting their foraging strategies or utilizing alternative resources in response to environmental changes (Winfree & Kremen 2009), which can enhance system persistence (Winfree et al. 2009). Resilience may be reinforced by pollinator behavioural plasticity, such as shifts in foraging strategies or alternative resource use, as well as by landscape connectivity, which facilitates pollinator movement between disturbed and undisturbed habitats (Hadley & Betts 2012). Furthermore, pollinator visitation frequency determines pollen transfer in specialized systems (Knight et al. 2005). Understanding the overall net effects (positive, negative, neutral) of extrinsic plant characteristics such as local density and pollinator spatial distribution on pollination success will provide insight into how mutualisms evolve and function. In particular, although highly-specialized pollination systems are typically more susceptible to disruptions, their co-adapted interactions may mitigate effect of reduced visitation thereby enhancing pollinator reliability under certain conditions, reducing pollination limitation and allowing for some degree of persistence even in highly disturbed environments (Muñoz-Gallego et al. 2022).

Here, we focused on the highly specific, nursery pollination system between the dioecious dwarf palm *Chamaerops humilis* and its specialized pollinator the weevil *Derelomus chamaeropis* (Curculionidae; Anstett 1999; Dufaÿ & Anstett 2004). Jácome-Flores et al. (2018) studied how the spatial patterns *C. humilis* affected the presence and abundance of *D. chamaeropis* larvae with limited mobility. However, it remains unknown how highly-mobile adult weevils respond to the local density and spatial distribution of their host plant. Thus, larvae and adult weevils differ in many relevant traits, including their contrasting mobilities. Whereas larvae are confined within their natal inflorescences, adults are highly flying and move among palms. Thus, factors shaping the spatial distribution of larvae (e.g., host density) should not necessarily be the same as those acting on adults. We therefore investigate for the very first time how the abundance of this pollinator in the adult phase relates with the spatial pattern of *C. humilis*. The aim of this work was to analyse how the *C. humilis* spatial patterns impinge the occupancy patterns of *D. chamaeropis* and their consequences on fruiting success of *C. humilis.* More specifically, we explored different hypotheses. (1) García et al. (2018) found that dwarf palm male inflorescences had more weevils than female plants, thus, we expected that adult weevil abundance will be positively related with male plants. (2) The spatial pattern of *D. chamaeropis* larvae over their host plants has been described as random, due the high mobility of adults, which enables them to move among host plants regardless of their highly aggregated spatial distribution (Jácome-Flores et al. 2018), thus, we expected that the adult weevil's spatial distribution will also be randomly distributed across reproductive palms. (3) Pollinator abundance is usually positively correlated to fruiting success, so we expect that female plants with higher abundance of adult weevils and co-pollinators (additional insect species that contributes to pollen transfer; García et al. 2018) will have higher fruiting success.

MATERIALS AND METHODS

STUDY SPECIES AND AREA

Chamaerops humilis is a small dioecious palm with pistillate and staminate inflorescences on different individuals (Herrera 1989; Anstett 1999). In Europe, it is common in coastal and subcoastal areas where it can live up to 1000 m above sea level (Herrera 1989), being part of different habitats like shrublands or at the understory of diverse forests (Merlo et al. 1993). The dwarf palm population of our study site (Jácome-Flores et al. 2016) shows a spatial pattern characterized by large clusters (radius: 21 m) including small aggregations (radius: 2.8-4 m) of individual palms. Previous genetic analysis showed that these clumps had lower inbreeding value (FIS value) with no spatial genetic structure (Jácome-Flores et al. 2019). *C. humilis* is a keystone species in the Mediterranean ecosystem, because it is very tolerant to disturbance (Herrera 1989), its strong potential for the restoration of native ecosystems and the recovery of ecosystem services (Garrote et al. 2019), and a valuable food resource for many mediterranean mammals and invertebrates (Muñoz-Gallego et al. 2019; Jácome-Flores et al. 2020). *C. humilis* is engaged in a nursery pollination with the host-specific palm flower weevil *D. chamaeropis* (Curculionidae, subfamily Derelominae) (Anstett 1999). Weevil larvae develop inside the rachis of the inflorescences (mainly male) where they stay in winter (Dufaÿ et al. 2004). On spring, adult weevils emerge from old dwarf palm inflorescences in search for inflorescences in anthesis (either female or male), where they typically stay until the end of anthesis, finding shelter, egg-laying sites and food (i.e. nectar droplets or pollen) (Dufaÿ et al. 2004). Adult weevils emerge mainly from staminate inflorescences and are mainly pollinivorous. Thus, *C. humilis* has two strategies to avoid sex selection from weevils and to ensure effective partner encounter and pollen transportation: odour mimicry (Dufäy et al. 2003) and flowering synchrony between sexes (Dufaÿ 2010). Larvae are confined within their natal inflorescences, adults are highly mobile, flying and moving among flowering palms (Jácome-Flores et al. 2018).

This study was conducted in the Doñana National Park (510 km2; 37°9′N, 6°26′W), on the right bank of the Guadalquivir estuary in south-west Spain. The study site was located at the Doñana Biological Reserve (DBR), the core area of the National Park. The climate is Mediterranean with some oceanic influence, with dry, hot summers (June-September) and mild, wet winters (November-February). The extreme drought is concentrated during the summer, and the main rainy period is during winter. Average annual rainfall is 549 mm, but varies widely, ranging between 170 and 1028 mm. Average annual temperature range between 15.4 and 18.7°C (data from Monitoring Team of Natural Process of Doñana Biological Station; http://icts.ebd.csic.es/datos-meteorologicos).

We selected a focal dwarf palm population within DBR, called Martinazo. This site is located in a transition zone between the Mediterranean shrubland and the marshland. Mediterranean type shrubland dominates the vegetation. This xerophytic shrubland is composed by *Halimium halimifolium*, *Rosmarinus officinalis*, *Ulex* spp., and *Stauracanthus* spp. Additionally, there are small patches of *Quercus suber* and *Olea europaea* var. *sylvestris* and *Fraxinus angustifolia* (Jácome-Flores et al. 2016). The plot area occupies 20.93 ha, where we georeferenced and marked all adult palm individuals (55 males and 41 females).

DATA COLLECTION

Dwarf palm flowering traits

In April of 2017, during the dwarf palm flowering peak (Jácome-Flores et al. 2018), we recorded plant sex (male or female) and inflorescences abundance (number of inflorescences produced by each reproductive individual). Additionally, we randomly selected and marked three pistillate inflorescences, and we counted all the flowers (flower display) of each reproductive female plant to monitor pollination success through fruiting success as a proxy (i.e., the number of fruit set divided by the number of flowers) (Fedriani et al. 2015).

Pollinator abundance

We established a systematic schedule for sampling pollinator activity, conducting observations from 9-11 a.m., coinciding with the peak of weevil activity. We recorded *D. chamaeropis* abundance (number of weevils on three inflorescences in the 96 focal dwarf palms) and the abundance of other co-pollinators, the pollen beetle *Meligethinus pallidulus* (Nitidulidae; García et al. 2018) and other Nitidulidae beetles, whose their peak activity matches with that of the main pollinator (Muñoz-Gallego et al. 2022). For both pollination types, we took a repeated sample of their abundance in two consecutive periods separated by one week (hereafter, Period A and Period B) within the pollination phenophase spanning the peak flowering of both sexes (maximum overlap period), although female ended their anthesis later (Jácome-Flores et al. 2018).

SPATIAL POINT PATTERN ANALYSIS

To assess the spatial distribution of *D. chamaeropis* and its potential effects on *C. humilis* fruiting success, we applied Spatial Point Pattern Analysis (SPPA), a robust statistical framework designed for characterizing fine-scale spatial distributions of "ecological objects" such as plants (Illian et al. 2008; Wiegand & Moloney 2014). SPPA works by analysing the georeferenced locations of individual plants, which can be supplemented with additional attributes that characterize the plants such as flower production, fruiting success, or pollinator abundance. Unlike simpler methods, which often rely on summary statistics or spatial averaging, SPPA enables a detailed examination of distance-dependent patterns, providing insights into how the measured attribute is shaped by the spatial distribution.

To examine potential distance dependence of the weevil abundance on *C. humilis*, we used techniques of quantitatively-marked point pattern analysis (Fedriani et al. 2015; Jácome-Flores et al. 2016). Our dataset comprises, for each individual dwarf palm, the coordinates, plant sex (male or female) and the weevil abundance as marks. We used a univariate and bivariate quantitatively-marked point pattern (Illian et al. 2008; Wiegand & Moloney 2014). Mark correlation functions are based on all (ordered) pairs of dwarf palms, which have interpoint distances r. The basic idea of the mark correlation function is then to estimate the mean value of a test function $t(m_i, m_j)$ of the two marks m_i and m_j, taken over all (ordered) pairs i-j of dwarf palms which have an inter-plant distance r. The univariate function cm(r) was performed for male and female plants separately. The function allows us to determine if plants with a nearby neighbour tend to host a higher number of weevils than the 'average' palm. The bivariate function cm2(r) was useful to determine if a female palm hosts fewer weevils when growing close to a male palm (compared to the 'average' female palm). We also used a variation of mark correlation function

Table 1. Summary statistics of GLMM. Female palms (F) and male palms (M).

Model	variables	estimate	*P*-value	R2 (%)
1. Weevil abundance	Inflorescences	0.008	<0.0001	12.52
	M palms	-0.031	0.636	
	F palms	2	0.0001	
2. Weevil abundance F palms	Inflorescences	0.013	<0.0001	40.38
	Flowers	0.0003	0.276	
3. Fruiting success	Inflorescences	-0.023	0.043	14.6
	weevil abundance	-0.016	0.088	
	Co-pollinator	0.016	0.982	

that directly relates the weevil abundance of *C. humilis* individuals to the density of their conspecific neighbours within a given distance, r. This "density correlation function" (for more details (Fedriani et al. 2015) $C_{m,K}(r)$ estimates the classic Pearson correlation coefficient between the weevil abundance m_i of a palm and the number of neighbours within distance r [$\lambda K_i(r)$].

SPATIAL PATTERN OF *CHAMAEROPS HUMILIS* FRUITING SUCCESS

To assess potential distance dependence of fruiting success in dwarf palms we used techniques of quantitatively-marked point pattern analysis. Our dataset includes all female dwarf palms and their fruiting success as a mark. Moreover, we independently assessed fruit set and flower display distance dependence. We estimated the mean fruiting success $\mu f(r)$ of female j that has a female i at distance r, divided by the mean fruiting success μf of all females, that is, $km(r)= \mu f(r)/\mu f$ (Wiegand & Moloney 2014). Thus, $km(r) > 1$ indicates that females that have females at distance r show, on average, higher fruiting success than expected at random. Conversely, $km(r) < 1$ indicates that females with other females within a distance r show, on average, reduced fruiting success compared to a random expectation. By using density correlation functions we also directly related fruiting success of *C. humilis* females to the density of their conspecific neighbours. This "density correlation function" (Fedriani et al. 2015) has the assumptions already described above.

To test the fit of the data with specific point process models, we fitted contrasting null models of the point processes and, using 199 randomizations, estimated simulated envelopes, being the fifth lowest and highest values of the summary statistics (Wiegand et al. 2013; Fedriani & Wiegand 2014). Observed values lying within the simulation envelopes would be indicative of stochastic patterns, according to the null model. Observed values above the top or below the bottom of the simulation envelopes indicate that such values were higher or lower than expected by the null model. To test the overall fit of the models, we used a Goodness-of-Fit (GoF) test that collects the scale-dependent information contained in the test statistic into a single parameter u_i, which represents the total squared deviation between the observed pattern and the theoretical result across the scales of interest. Therefore, the GoF test returns a P-value that, when significant, indicates a departure of the observed mark correlation function from the random marking null model over the distance interval of interest. If a significant departure occurs, we can inspect the plot of the mark-correlation function together with the simulation envelopes to identify the specific distances r where departures occurred. For all point pattern analysis, we used the software package *Programita* (Wiegand & Moloney 2014) which can be accessed at https://www.programita.org.

STATISTICAL ANALYSIS

We used a Spearman correlation test to assess the relation between weevil abundance in periods A and B. We used a Mann-Whitney U test to determine differences in weevil abundance between plant sexes at periods A and B.

For the statistical analysis of the response variables of weevil abundance and fruiting success we performed Generalized Linear Mixed Models (GLMM). For weevil abundance on each palm (model 1), we used a Poisson GLMM with a *log* link function, including plant sex and number of inflorescences as explanatory variables. For weevil abundance on female palms (model 2), we used a Poisson GLM with a *log* link function, using number of flowers and inflorescences as explanatory variables. For fruiting success, we used a *binomial* GLMM with *logit* link function, including number of inflorescences, presence of co-pollinators and mean weevil abundance as explanatory variables. Individual plants were used as a random factor.

RESULTS

PRESENCE AND ABUNDANCE OF *DERELOMUS CHAMAEROPIS*: DWARF PALM SEX AND SAMPLING PERIOD

We recorded a total of 942 and 1,479 individual weevils in the two repeated weevil censuses of every palm (period A and period B, respectively). Adult weevils were more frequently found on male (88% of palms with at least 1 weevil) compared to female palms (67%; Tab. 1). The percentage of weevil presence was rather variable among periods, with more weevil presence in period B (86%) compared to period A (72%). Presence in female and male palms between periods was also higher in period B (83% of all females; 89% of all males) than in A (51% of all females; 87% of all males).

We found a significant, positive correlation in the number of weevils between A and B periods (Spearman correlation, rho= 0.20 $P < 0.05$, $N = 96$) suggesting a temporal consistency in weevil counts across individual palms. A Mann-Whitney test further indicates no significant differences (W= 4161, $P = 0.24$, $N1 = N2 = 96$) between the counts at individual plants (paired counts) between both periods. Moreover, we found significant differences (W = 5836, $P < 0.05$, $N1 = N2 = 96$) in weevil abundance between male and female dwarf palms (Fig. 1). Weevil abundance in female plants was 14 ± 3.7 individuals and 11 ± 1.3 individuals in male plants (95% confidence intervals of the means were (4.6, 23.5) and (11.3, 16.8), respectively). We found a significant difference (W = 10986, $P = 0.01$) between female palms in A and B periods (Fig. 1), yet with no differences between male palms (W = 1433 $P = 0.63$).

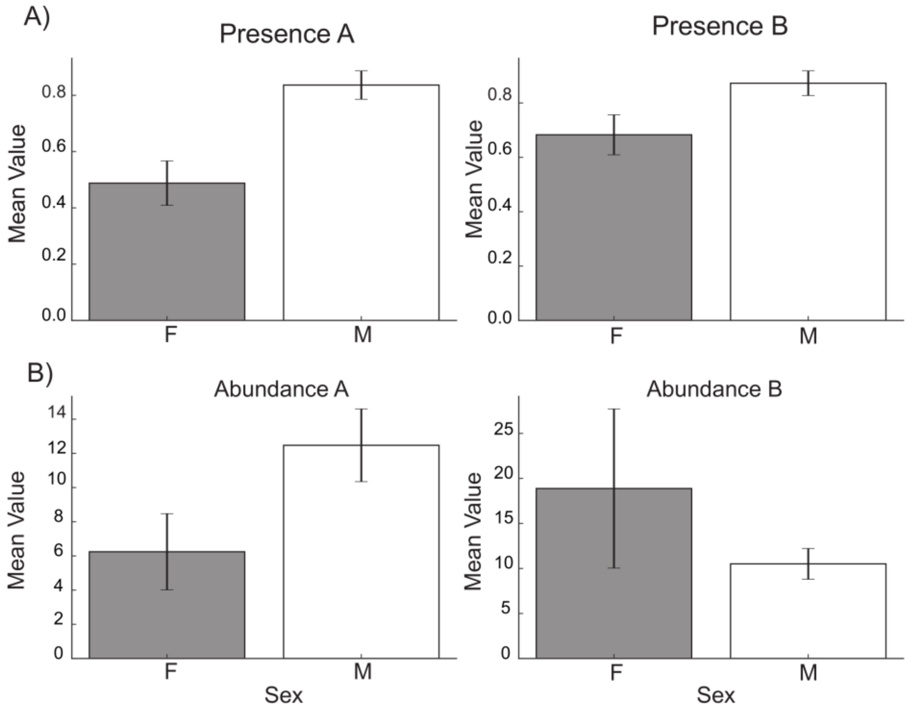

Figure 1. A) Weevil presence ± SE in each sampled period and palm sex and B) Weevil mean ± SE abundance in each sampled period and palm sex. Grey bars represent female palms and white bars represent male palms.

WEEVIL ABUNDANCE AND PLANT POLLINATION SUCCESS: EFFECT OF FLOWERING TRAITS AND CO-POLLINATORS

We monitored the fruiting success of 19,845 flowers in female dwarf palms. On average, each plant produced 20.6 inflorescences (s.e. ± 3.4), with each inflorescence bearing an average of 185.4 flowers (s.e. ± 30.9). The mean overall fruiting success (±1 s.e.), calculated as the proportion of flowers that developed into fruits, was 0.15 (s.e. ± 0.3). For the weevil abundance model (model 1), the number of inflorescences had a significant positive effect on weevil abundance (effect estimate = 0.008, $P < 0.001$; Tab. 1). Female palms had a high and significant positive effect (effect estimate = 2, $P < 0.001$; Tab. 1) on weevil abundance. In the model assessing weevil abundance specifically on female palms (model 2), the number of inflorescences had a significant and positive effect (effect estimate = 0.13, $P < 0.001$; Tab. 1), while the number of flowers had no effect (effect estimate = 0.0003, $P = 0.276$; Tab. 1). For the fruiting success model (model 3), the number of inflorescences had a slight yet significant negative effect on fruiting success (effect estimate = -0.02, $P = 0.043$; Tab. 1). The effect of weevil abundance on fruiting success was marginally significant (effect estimate = -0.016, $P = 0.088$; Tab. 1), while the presence of co-pollinators did not influence fruiting success (effect estimate = 0.016, $P = 0.982$; Tab. 1).

SPATIAL PATTERN OF *D. CHAMAEROPIS*

We performed analyses of *D. chamaeropis* spatial patterns using the r-mark correlation function *k*m(r), with and without accounting for sex expression. There was no significant aggregation of weevil abundance at any spatial scale neither between male (rank = 76, $P = 0.63$; Fig. 2A) and female plants (rank = 145, $P = 0.28$; Fig. 2B), nor across sexes (rank = 106, $P = 0.48$; Fig. 2C). Without sex as mark along all *r* distances considered, distance had no significant effect on abundance (rank = 106, $P = 0.18$; Fig. 2D).

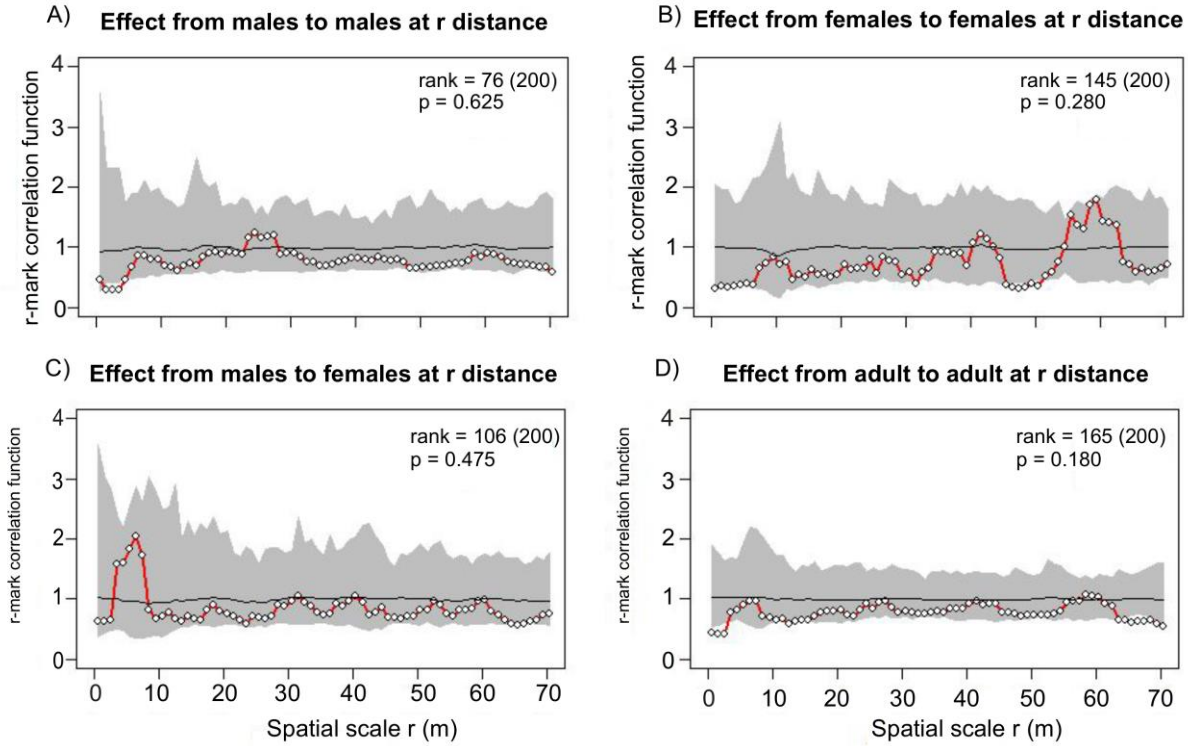

Figure 2. Mark correlation function analyzing spatial association of the weevil abundance in dwarf palm study population with and without sex pattern. In analysis with sex pattern, the "univariate" r-mark correlation function estimates the mean weevil abundance of male palm (type 1) that have another male palm at distance r. The "bivariate" r-mark correlation function estimates the mean weevil abundance of male palm (type 1) that have female palm at distance r. The observed data is represented by white circles. In analysis without sex pattern, r-mark correlation function estimates the mean weevil abundance of adult palm that have another adult palm at distance r. The expected mark correlation function is the black line; grey polygon: expectation under the null model, that is limited by simulation envelopes being the fifth lowest and highest values taken from 199 simulations of the null model where both sexes were independently randomized.

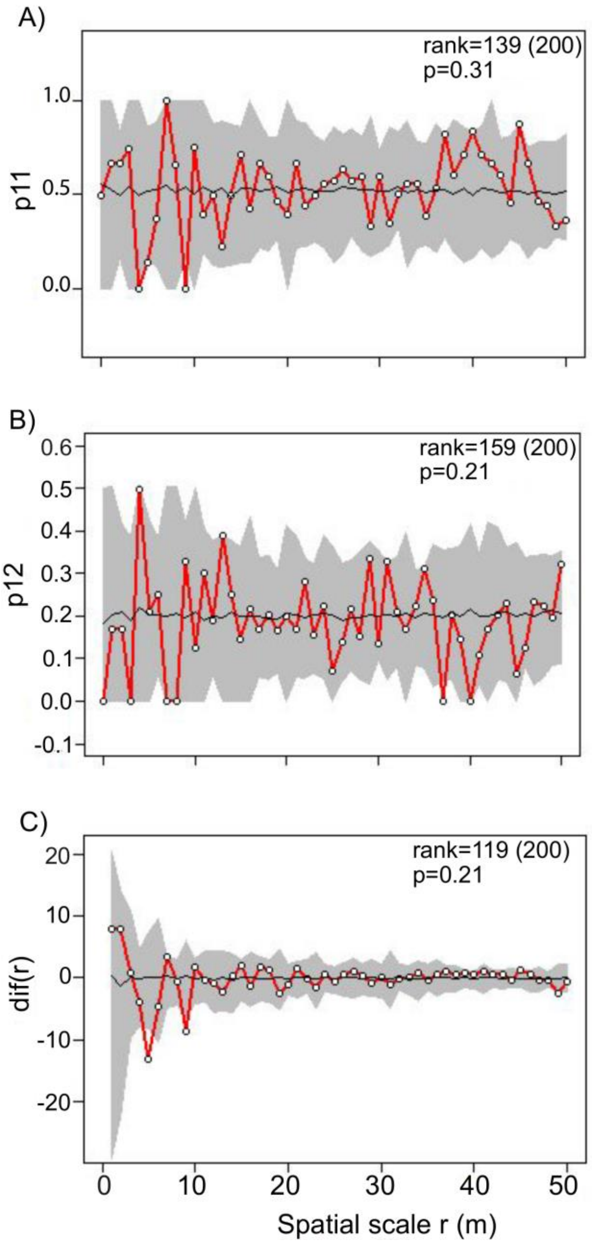

Figure 3. Analysis of weevil presence absence in our study population with random labeling function. A) Function *p*11(r) gives the conditional probability, that for two dwarf palms separated by distance r, both are type 1 (i.e. with weevil presence). B) Function *p*12(r) gives the conditional probability, that for two dwarf palms separated by distance r, the first type 1 (i.e. with weevil presence) and the second type 2 (i.e. without weevil presence). C) Function *dif*(r) compares the density of dwarf palms (i.e. 1+2) around dwarf palms with weevil presence (i.e. type 1) with the density of palms (i.e. 1+2) around palms without weevil presence (i.e. type 2). The expected value of this test statistics is zero under random labelling null model. The observed data is represented by white circles. The expected mark connection function is black line; grey polygon: expectation under the null model, that is limited by simulation envelopes being the fifth lowest and highest values taken from 199 simulations of the null model.

The random labelling analysis showed that presence of weevils did not correlate with dwarf palm aggregation or spatial pattern (Fig. 3). The univariate function *p11(r)*, showed no signs of significant aggregation (rank = 139, *P* = 0.31; Fig. 3A). The bivariate function *p12(r)*, indicated no spatial aggregation between palms with and without weevils (rank = 159, *P* = 0.21; Fig. 3B). The results of test *dif(r)*, showed that palms with weevil presence were not associated with palm clusters (rank = 119, *P* = 0.41; Fig. 3C).

The density correlation function *Cm,k(r)*, taking into account sex expression, showed no effect of neighbourhood density of same sex conspecifics on weevil abundance. There was no significant effect of male (rank = 143, *P* = 0.29; Fig. 4A) or female (rank = 145, *P* = 0.28; Fig. 4B) focal palms related to their conspecific neighbourhood density. Regarding the neighbourhood density of all palms, we found a significant, negative, density-dependence response of weevil abundance (rank = 192, *P* = 0.045; Fig. 4C).

SPATIAL PATTERN OF *CHAMAEROPS HUMILIS* FRUITING SUCCESS

The density correlation function *Cm,k(r)* showed a significant and positive relation for the fruiting success of female palms at scales up to 5 m (rank = 198, *P* = 0.015; Fig. 5A) and for the number of fruits at scales between 5-15 m (rank = 198, *P* = 0.015; Fig. 5B) within this specific range of neighbourhood density. The r-mark correlation function *km(r)* indicated significant positive distance dependence at small scales (2-5 m) for fruiting success (rank = 200, *P* = 0.005; Fig. 5D). For fruit number, a positive relation was observed at both small (3-5 m) and large scales (63-70 m) (rank = 197, *P* = 0.020; Fig. 5E). For flower number, both density correlation (rank = 55, *P* = 0.730; Fig. 5C) and r-mark correlation (rank = 170, *P* = 0.150; Fig. 5F) functions showed no significant relation.

DISCUSSION

Our study addresses the spatial dynamics of the nursery-pollination system of the dwarf palm *Chamaerops humilis* and its specific pollinator, the weevil *Derelomus chamaeropis*. We found that the presence and abundance of the adult weevil *D. chamaeropis*, depend more on the sex of the plant than on plant spatial distribution. While male palms are more likely to host weevil larvae, female palms attract substantial numbers of adult weevils.

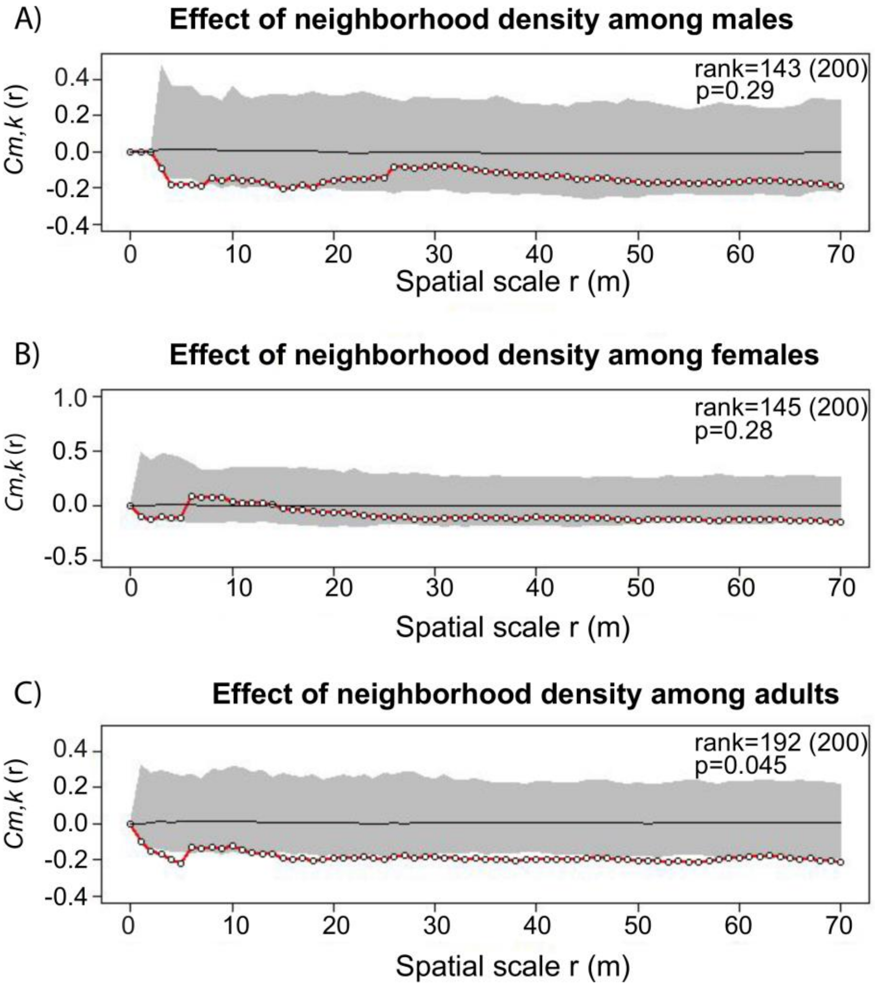

Figure 4. Mark and density correlation function analyzing spatial distance and density processes of the fruiting success, fruit number and flower number in the dwarf palm study population. More details about simulation envelopes in Figure 2.

The plants neighbourhood density had a significant negative effect on weevil abundance, where higher neighbourhood density of palms resulted in reduced local abundance of weevils. In contrast, we found enhanced pollination success in denser patches with close neighbouring palms suggesting a spatial decoupling between pollinators abundance and reproductive success.

The female inflorescences of the dwarf palm produce resin droplets as a defence mechanism during fruit development (Anstett 1999; Fedriani & Delibes 2011), that reduce the number of developing larvae (Jácome-Flores et al. 2018). This plant strategy aims to avoid significant damage to the rachis of the inflorescence and, consequently, improve reproductive success. Weevils avoid visiting and ovipositing in non-rewarding pistillate inflorescences. However, both female and male plants produce the same odour signals, making it impossible for adult weevils to distinguish between deceptive females and rewarding males (Dufaÿ et al. 2003). Contrary to our predictions, although we found a high occurrence of weevils on male palms, we observed higher adult abundance in females than in male palms. When comparing adult weevil abundance between anthesis periods (A and B), we recorded a higher number of weevils on female inflorescences in the second period. Male dwarf palms tended to flower more synchronously, and females ended their anthesis later, with some overlap with male flowering (Jácome-Flores et al. 2018). This suggests that a large number of weevils, attracted by odour signals during flower anthesis (see (Dufaÿ et al. 2003), moved from males without available inflorescences to late-flowering female palms, increasing their abundance there. These mechanisms, including odour mimicry and male-female asynchrony, underscore how both sexes contribute to supporting weevil populations while ensuring pollination services—males as primary

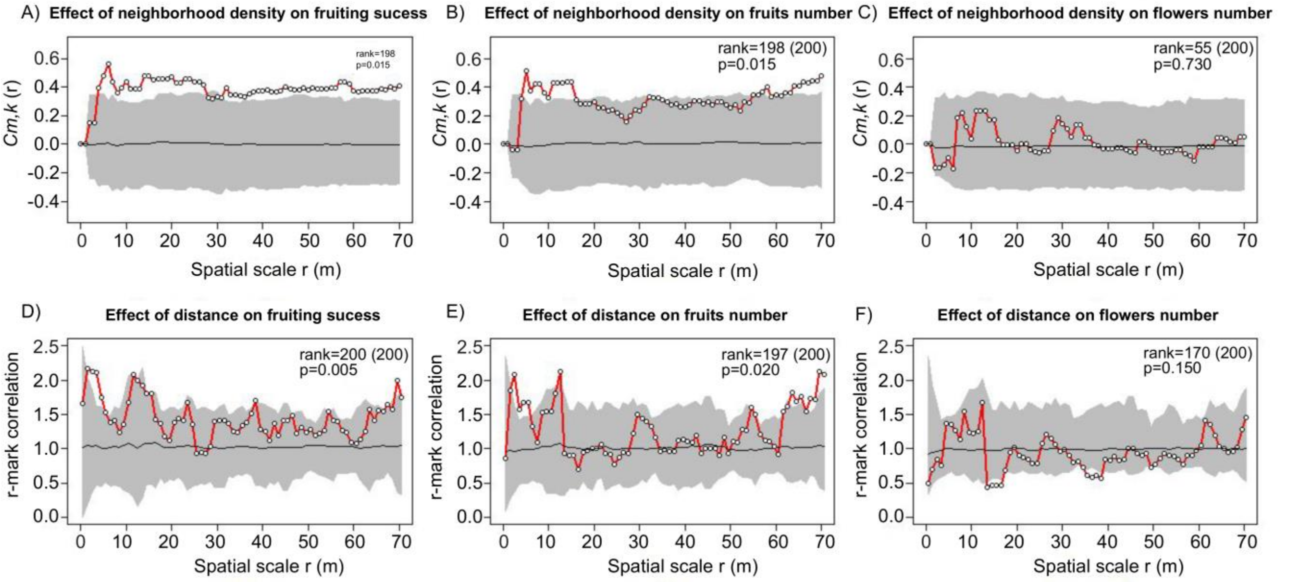

Figure 5. Density correlation function analysing spatial association of the weevil abundance in dwarf palm study population with and without palm sex as mark. More details about simulation envelopes in Figure 2.

larval hosts and females as attractants (Jácome-Flores et al. 2018).

In terms of spatial patterns, our results confirmed our initial predictions on how the spatial patterns of host plants could influence movement and pollinator attraction. We detect no significant spatial clustering regarding adult weevils. Two interrelated explanations could account for this observation: the high mobility of weevils and the random spatial pattern of the floral resources. As for weevils' mobility, previous observation demonstrated that weevils are capable to travel distances up to 235 m (Jácome-Flores et al. 2018). Such distance clearly surpassed the maximum distance of the more isolated palm within the population (50m) (Jácome-Flores et al. 2016). As for the floral resource, our SSPA analysis showed that, although the dwarf palms show an intense aggregated pattern (Jácome-Flores et al., 2016), the inflorescences display appears randomly in space. This seems to be a pattern in specialized pollination mutualisms, where pollination success is driven more by pollinator behaviour than by host plant spatial structure. Previous studies on other nursery pollination systems such as *Lophocereus–Upiga* (Holland & Fleming 1999) and *Trollius–Chiastocheta* (Klank et al. 2010) showed also no direct effects of plant spatial distribution on pollination success. Similar trends have been observed in other specialized mutualisms, such as fig–fig wasp (Harrison & Yamamura 2003) and yucca–yucca moth interactions (Wilson & Addicott 1998), where pollination success is determined more by pollinator behaviour rather than plant spatial structure.

Previous studies of pollination systems have been identified consistent trends for a high number of inflorescences attracting greater numbers of pollinators (Knight et al. 2005; Nattero et al. 2011). In our study population, the abundance of adult weevils at individual palms was positively related with female palms and number of inflorescences. Interestingly, our study revealed an interesting contrast in the relationship between adult weevil abundance and larval presence on *C. humilis* in relation to inflorescence number, further shaped by the sex of the palm. Jácome-Flores et al. (2018) found that plants (mainly male) with a high number of inflorescences had a lower probability of holding weevil larvae. In contrast, we found that adult weevils were more abundant on plants (mainly females) with a high number of inflorescences. This pattern suggests a divide between adult and larval habitat suitability. Adult weevils are attracted to palms with abundant inflorescences, regardless of whether these palms are suitable for larval development. Male palms with fewer inflorescences may offer concentrated resources that favour larval growth, while female palms attract adults for resources but prevent larval development (Jácome-Flores et al. 2018). This separation ensures that adult weevils find plentiful resources across both sexes, while larvae develop mainly on male palms where they face less direct competition for concentrated resources.

Pollinator attraction in dwarf palms may depend not only on inflorescence abundance but also on leaf odour emissions (Dufaÿ et al. 2003). If inflorescence abundance correlates with leaf density or emissions, weevil attraction would be an indirect consequence of leaf-mediated chemical signalling. Additionally, when we explored the effects of density-dependence at the plant level, we found a negative effect of density- and distance-dependence of plants on adult weevil abundance. Thus, while adult weevils respond positively to high inflorescence numbers on individual palms, high neighbourhood density appears to dilute resources where plants could experience high competition for adult weevils (e.g., Alonso-López et al. 2022), leading to a decrease adult weevil abundance locally.

There is an interesting relationship between weevil abundance and plant density. While there was a negative correlation between the two, we observed that plants in high-density neighbourhoods exhibited increased fruiting success and number of fruits. This suggests that weevils may be more effective in pollen transfer in high-dense patches due to two main factors: first, weevils spent less effort searching for plants, and second, there was reduced competition among pollinators for the plants' resources (e.g., Fedriani et al. 2015). However, we must be cautious with these fruiting success results, considering that we investigated a small *C. humilis* population.

Factors such as soil resource availability, intraspecific competition, or co-pollinators could potentially impact fruit initiation and development, and overall fruit set (Thompson et al. 1992; Fedriani et al. 2015; García et al. 2018). The involvement of co-pollinators has been described in some specialist pollination systems. For example, in *Senita* cacti, active pollination by the nursery pollinating moth mutualism is well-documented (Holland & Fleming 1999), and the role of co-pollinator bees in fruit set is environmentally dependent (Holland & Fleming 2002). Despite the apparent specialization for pollination by weevils (Dufaÿ & Anstett 2003; Dufaÿ et al. 2004; Dufaÿ 2010), dwarf palms have not evolved floral traits that exclude all other pollinators. We collected the dwarf palm co-pollinators *Meligethes rotundicolis* and *Meligethinus humeralis* (Audisio et al. 2009; Baviera & Audisio 2014; García et al. 2018). Although both species have the potential to influence fruit set, our results indicate no significant effect on fruiting success, suggesting a limited contribution. However, further exclusion pollination experiments are required to corroborate this finding.

In summary, our results indicate that the presence and abundance of adult weevils are more determined by plant sex, number of inflorescences and anthesis periods, rather than by plant clustering spatial patterns. However, local neighbourhood density had a significant effect, with higher densities correlating with reduced weevil abundance, suggesting a balance in weevil distribution shaped by local resource availability and competitive interactions, rather than by the broader spatial arrangement of palms. In terms of pollination, despite the negative density-dependence effect of weevil abundance, we found evidence of positive distance-density dependence among female palms in their fruiting success, suggesting that dense patches may enhance pollination efficiency and fruit set, potentially by reducing search effort and competition among pollinators. This spatial decoupling between pollinator distribution and reproductive success highlights the complex dynamics of this nursery pollination system. The differences between the spatial patterns of the specialist pollinator and fruiting success at small spatial scales raise questions about the possible implications of co-pollinators on pollination services in the dwarf palm. In particular, studying potential co-pollinators and their spatial arrangement across the population would complement the results of our work. Our findings on the spatial pattern in both participants of this nursery pollination system contribute to understanding the mutualism between *C. humilis* and *D. chamaeropis*, revealing the presence of long-distance pollen transfer and random-like patterns of weevil presence on plants. Interestingly, our results support the idea that, high pollinator mobility decouples plant spatial structure from pollination success, as seen in other specialized nursery pollination systems.

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AUTHOR CONTRIBUTION

Concept and design MJF, PJ & JMF, data collection MM, GC & MJF, data analysis MM & MJF, writing MM, MJF, PJ, JMF & GC, edits and approval for publication MM, MJF, PJ, JMF & GC.

DISCLOSURE STATEMENT

All authors declare no potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data used to write this article are available at 10.5281/zenodo.14137785.

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