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The Eurasian badger-generated seed rain drives the natural (re)colonization of vacant human-altered areas by a keystone pioneer palm

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ABSTRACT

Seed dispersal is an essential ecological process for plant (re)colonization, especially in intensively human-altered habitats such as old-fields (i.e. abandoned farmlands) where seed arrival is often limited. Assessment of spatial patterns of mammal-generated seed rain and their matching with the spatial distribution of adult plants provides essential information on the patterns and pace of the (re)colonization processes. For instance, increased seedling survival far from adult plants could indicate density-dependent mortality (Janzen-Connell) effects whereas increased survival close to adult plants could suggest facilitative effects. Here, we characterized during two dispersal seasons the spatial distribution of feces from four frugivorous mammals and quantified its spatial association with the distribution of adult plants of the pioneer Mediterranean dwarf palm (*Chamaerops humilis*) in two old-fields in southwestern Spain. We also estimated the dispersal kernels of both emerged and surviving seedlings and assessed potential evidence for Janzen-Connell and/or facilitative effects. Using a spatially explicit approach, we revealed strong differences between study sites in the strength and scale of spatial associations between mammal feces with *C. humilis* seeds and adult dwarf palms, being strongly positive at small scales in one site and slightly positive at larger scales in the other one. Further, we found some evidence of both Janzen-Connell and facilitative effects depending on the study site. Altogether, our results emphasize the central role as seed disperser of the Eurasian badger (*Meles meles*) in the natural (re)colonization of Mediterranean old-fields and the spatial variations of the underlying mechanisms and demographic consequences for plant populations.

1. Introduction

Seed dispersal is a central ecological process for plant population dynamics and community assembly (Nathan and Muller-Landau, 2000; Herrera, 2002; Wang and Smith, 2002; Schupp et al., 2010). It is especially critical for the (re)colonization of human-altered habitats where seed arrival is often limited (e.g. abandoned farmlands; Pugnaire et al., 2006; Charles et al., 2017; but see Knappová et al., 2017). Restricted seed rain into human-altered areas due to lack of either seed sources (Török et al., 2018) and/or seed dispersers (Pérez-Méndez et al., 2016) strongly limits natural (re)colonization. On this matter, it is widely recognized that vertebrate frugivores often play a decisive role in dispersal processes of many plant populations and communities (Levey et al., 2002; Côrtes and Uriarte, 2013; Bascompte and Jordano, 2014; Traveset et al., 2014). For instance, frugivorous mammals ensure seed arrival to vacant, open, human-altered areas (e.g. old-fields; Escribano-Ávila et al., 2015), generating a seed rain that strongly affects population recruitment and eventually the spatial distribution of reproductive individuals (e.g. Fedriani et al., 2010; Escribano-Ávila et al., 2014; García-Cervigón et al., 2017). Besides, animal-generated seed rain usually establishes the initial template on which post-dispersal processes (e.g. seed and seedling mortality) are manifested. Therefore, assessing spatial patterns of potential seed rain generated by frugivores and their matching with spatial distribution of adult plants can provide useful information about the underlying mechanisms that determine the spatial distribution of seedlings, saplings, and adults (Zhu et al., 2013; Lara-Romero et al., 2016; Perea et al., 2021).

The distance between seeds/seedlings and conspecific adults is often an important determinant of recruitment success. On the one hand, the

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Janzen-Connell hypothesis posits that with increasing distance from the adult, the density of seeds/seedlings decreases, and their survival increases due to a reduced impact of distance- and density-responsive enemies (Connell, 1971; Janzen, 1970). Therefore, we could expect a greater seedling recruitment probability far from conspecific adults than near them (Comita et al., 2014; but see Hyatt et al., 2003). On the other hand, positive effects for seedlings may occur in the vicinity of adult conspecific plants especially under stressful abiotic conditions (Filazzola and Lortie, 2014). Thus, we could expect greater seedling recruitment near adults (i.e. nursing effect, *sensu* Callaway, 2007). Alternatively, both types of effects could counteract each other resulting in no net demographic consequences of distance to adult conspecifics. To explore the extent to which density-dependent mortality (Janzen-Connell) and/or facilitative effects impact plant recruitment during (re)colonization events, we need to assess the dispersal kernels and recruitment in relation to the distance to nearest adult plant. The potential establishment site where seeds arrive and seedlings emerge is named the 'basic dispersal kernel' (i.e. transition from seed to emerged seedling) (*sensu* Nathan et al., 2012). Then, a portion of these seedlings survives after a specific time (e.g. one year) becoming saplings ('effective dispersal kernel', i.e. transition from emerged seedling to surviving seedling) (*sensu* Nathan et al., 2012).

The ecological filters influencing plant recruitment success (e.g. post-dispersal seed predation, microhabitat suitability for seedling emergence and survival, herbivory; Gómez-Aparicio, 2008; Hampe et al., 2008; Garrote et al., 2022) largely depend on the spatial patterns of seed deposition by dispersers (e.g. García-Cervigón et al., 2017), which often vary in space and time. In this regard, to fully comprehend the context-dependent variation of frugivore-generated seed rain and its consequences for recruitment, variation among disperser species, study sites, and seasons must be considered (e.g. Perea et al., 2013; Donoso et al., 2017; Loayza et al., 2020).

In this study, we quantified the spatial associations between the potential seed rain generated by four frugivorous mammals and the distribution of adult Mediterranean dwarf palms (*Chamaerops humilis*, Arecaceae). Besides, we also estimated the kernel of emerged seedlings (i.e. basic dispersal kernel) and that of surviving seedlings (i.e. effective dispersal kernel) (*sensu* Nathan et al., 2012) in relation to the distance to the nearest conspecific adult reproductive female palm. This pioneer mammal-dispersed palm plays a keystone ecological role in the (re) colonization of Mediterranean human-altered areas because of its strong interspecific facilitative effect, boosting establishment of numerous woody plant species (Garrote et al., 2019, 2021). In our study region, fruits of this keystone palm are mostly consumed by medium-sized carnivores and ungulates (Fedriani and Delibes, 2011; Selwyn et al., 2020). Differences among frugivore species in their relative abundance, mobility, frugivory level, and fecal marking behavior (Jordano and Schupp, 2000; Sakamoto and Takatsuki, 2015; Cancio et al., 2017; Fedriani et al., 2018) can yield variation in the pattern and scale of seed rain and in its effect on seedling recruitment and establishment.

The assessment of spatial relationships between the spatial distribution of mammal feces (many of them comprising seeds) and pioneer keystone plants using a spatially explicit approach may have a vital importance for the comprehension of patterns (e.g. density-dependent effects) driving the natural (re)colonization of human-altered areas. To this end, we used recent extensions of spatial point pattern analysis (SPPA, hereafter) that constitute a powerful approach to quantify spatial associations among multiple point patterns (e.g. dispersed seeds, adult plants) at a range of spatial scales (Illian et al., 2008; McIntire and Fajardo, 2009; Wiegand and Moloney, 2013). More specifically, we used spatial data of both fresh mammal feces and adult dwarf palms that were systematically georeferenced during two consecutive seed dispersal seasons in two old-fields within the Doñana National Park (SW Spain). We addressed the following specific questions: (*i*) Are mammal feces spatially associated between seed dispersal seasons and, if so, at what spatial scale? (*ii*) Are mammal feces spatially associated with adult palms and, if so, at what spatial scale? (*iii*) Are mammal feces with *C. humilis* seeds spatially associated with adult palms and, if so, at what spatial scale? Finally, we assessed evidence of both Janzen-Connell and facilitative effects by monitoring seedling survival near and away from mother plants. By examining two study sites that differ in their human-management history (Garrote et al., 2019) and the relative abundances of target mammal species (e.g. Garrote et al., 2018), we evaluated potential spatial variation in the scale and strength of spatial associations and density-dependent seedling mortality.

2. Materials and methods

2.1. Study area and sites

The study was conducted during dwarf palm's seed dispersal seasons (October-December) of 2017 and 2018 in the Doñana National Park (37°9′N, 6°26′W; SW Spain). The climate is Mediterranean sub-humid, characterized by hot, dry summers and mild, wet winters (see a detailed climatic description in Żywiec et al., 2017). The Doñana area is a human influenced and fragmented landscape, in which suitable habitat patches (e.g. scrubland) are isolated by cultivated fields, towns, marshes, or dunes (Fedriani et al., 2010). Specifically, the Doñana area comprises two main environments: Mediterranean scrubland and marshland. Scrubland constitutes a patchy, heterogeneous landscape with a great variety of different habitats whereas marshland remains flooded for part of the year (Fedriani and Wiegand, 2014).

We selected two study sites, called 'Matasgordas' (64.5 ha) and 'Reserva' (21.4 ha) (10 km apart), dominated by scattered *Quercus suber* and *Olea europaea* var. *sylvestris* trees within a composition of both dense Mediterranean scrubland (*Halimium halimifolium, Stauracanthus genistoides* and *Ulex* spp.) and an open pastureland. Original landscapes were 'dehesas' (i.e. agrosilvopastoral systems occupied by scattered oak trees; *sensu* Joffre et al., 1988) with Mediterranean scrubland understory. These sites were strongly transformed into open pasturelands with patches of scrubland for their intensive exploitation for cultivation and livestock ranching, although there were differences in the human management (Fedriani et al., 2018; Garrote et al., 2019). In Matasgordas, most trees and shrubs were mechanically removed in 1970 to facilitate intensive cow grazing until 1996, when the area was expropriated and protected by the Spanish National Park Service, and the cows removed. In Reserva, there was a more intensive and harsher human management of the landscape. Specifically, most trees were cut down and controlled plowing applied every 25–30 years until 1964, when the area was declared a Biological Reserve and cultivation and livestock ranching were finished. Despite this, intensive cattle grazing persists in the area. Nowadays, both sites represent old-fields that since their inclusion within the National Park are being (re)colonized by several animal-dispersed native plants such as *C. humilis, Pistacia lentiscus, Rubus ulmifolius* or *Pyrus bourgaeana* (Fedriani et al., 2018; Garrote et al., 2019).

2.2. Study species

The Mediterranean dwarf palm (*Chamaerops humilis*) is endemic to the Western Mediterranean basin (Guzmán et al., 2017). This dioecious palm blooms during March-May and is mostly pollinated by insects (García et al., 2018; Jácome-Flores et al., 2018; Muñoz-Gallego et al., 2022). Fruits are 'polydrupes' comprising one to three drupes which are independent dispersal units. Fruits are attached to dense infrutescences of up to 30 cm long (7–120 fruits per infrutescence; Selwyn et al., 2020) and are located at ~10–30 cm from the ground level. The seed dispersal season ranges from September to December. Seeds (0.6–0.8 g, 16.3 ×11.0 mm average size; Muñoz-Gallego et al., 2019) are mainly dispersed by medium-size carnivores such as Eurasian badgers (*Meles meles*) and red foxes (*Vulpes vulpes*) (Fedriani and Delibes, 2011; Selwyn et al., 2020). While badgers show similar abundances in both study sites, red foxes were more abundant in Reserva than in Matasgordas (Table 1). Wild boar (*Sus scrofa*) are considered fruit predators (Garrote et al., 2018), although they sporadically disperse some viable seeds (Fedriani et al., 2018). Similarly, red deer (*Cervus elaphus*) act as seed predators, grinding most ingested seeds (Fedriani and Delibes, 2011), although they occasionally can disperse some viable seeds by regurgitation (Castañeda et al., 2018). Abundance of both ungulate species was similar between study sites and always much larger than carnivore abundance (Table 1).

Germination of *C. humilis* seeds is hypogeal and remote, with most seedlings emerging during the following spring and the early summer (i.e. after 6–7 months of being dispersed). In the Doñana area, seedlings are frequently observed emerging from both fresh and old (>1 year) feces (Fedriani and Delibes, 2011). Seedling desiccation is high during the first summer due to severe droughts (~70–80%; Authors, *unpublished data*). Nevertheless, we have detected approximately half of these desiccated seedlings resprout after the first rains in the fall (~50–60%; Authors, *unpublished data*). The dwarf palm shows no soil preferences, but it avoids floodable areas (Jácome-Flores et al., 2016). This palm usually forms hotspot of recruitment thanks to its capacity to facilitate other plant species (Garrote et al., 2021). The distribution of *C. humilis* shows a marked double-clustered spatial pattern with small clusters of a radius 4.2 – 6.0 m (2.1 – 6.8 palms·cluster^{-1}) nested within large clusters with 29.1 – 39.1 m radius (28.9 – 42.6 palms·cluster^{-1}) (Garrote et al., 2019).

2.3. Mammal fecal surveys

From October to December of 2017 and 2018, we conducted on average ~1 transect daily (range = 0 – 4) searching for mammal feces in each study site. The target mammal species were the four main consumers of *C. humilis* fruits: badger, red fox, wild boar, and red deer. These mammals differ in their spatial and fecal marking behaviors. Badgers recurrently defecate at latrines where they partially or totally bury the feces (and dispersed seeds within them) though they occasionally may deposit some spatially isolated feces. Badger feces show a highly clustered distribution at short spatial scales (Fedriani and Wiegand, 2014). Red foxes mark their territories by defecating at highly prominent sites (e.g. edge of unpaved roads; Suárez-Esteban et al., 2013). Red fox feces have a spatially random distribution (Fedriani and Wiegand, 2014). Wild boar feces tend to be slightly clustered, while red deer feces are usually spatially scattered (Fedriani et al., 2010). However, the feces of wild boar and red deer were grouped into 'ungulates' for the spatial point pattern analyses since they both usually act as predators of *C. humilis* seeds. Mammal feces were identified at the species level based on their size, shape, odor, and color (Fedriani et al., 1999). We made a significant effort to distribute our sampling effort homogeneously across each study plot. Specifically, we set a total of 24 and 15 regularly distributed 'starting points' (100 m apart) within Matasgordas and Reserva respectively. During each transect, an observer walked from a starting point (which changed among consecutive surveys by rotating them clockwise) to the opposite side of the plot following a non-fixed zigzag path recording mammal feces within a radio of 5 m from the observer (i.e. width = 10 m). Then, the observer came back following a different path to a changing location of the departure plot side (Fedriani and Wiegand, 2014).

Table 1
Abundance of mammal species in both study sites. The abundance is measured as the average number of individuals detected per survey (the number of surveys are shown in parentheses for each species). Surveys were carried out by the Natural Processes Monitoring Group (Doñana Biological Station) in March, June and September from 2010 to 2019. Surveys were conducted by off-road vehicle (10–15 km·h^{-1}) with the observes placed on the car's roof rack (i.e. 3 m above ground level). Two surveys were taken every monitoring day, the first started one hour before sunset and the second, one hour after sunset (the observers used spotlight in nocturnal surveys). The length of surveys was 14.8 and 14.4 km in Matasgordas and Reserva, respectively.

Mammal species	Matasgordas	Reserva
Cervus elaphus	3.93 ± 0.32 (N = 584)	2.31 ± 0.12 (N = 507)
Sus scrofa	2.06 ± 0.26 (N = 93)	2.34 ± 0.26 (N = 82)
Meles meles	0.06 ± 0.03 (N = 54)	0.02 ± 0.02 (N = 48)
Vulpes vulpes	0.11 ± 0.04 (N = 55)	0.48 ± 0.07 (N = 60)

At Matasgordas, each survey took about 1.25 h and we undertook 97 surveys (65 and 32 in 2017 and 2018 respectively; 137.5 observer hours), with an average length of 3.3 ± 0.1 km. The total distance covered was 308 km (Fig. A.1a). At Reserva, each survey took about one hour and we undertook 97 surveys (65 and 32 in 2017 and 2018, respectively; 91.2 observer hours) with an average length of 1.9 ± 0.1 km. The total distance covered was 176 km (Fig. A.1b). Since the number of mammal feces found per fecal survey in 2018 was much lower than in 2017, we considered the lower sampling effort employed during this season to be adequate to record in detail the pattern of seed rain. All fresh feces were georeferenced in each transect using a submetric GPS Leica 1200, and tagged (Fig. A.2). For each scat, we recorded sampling day, transect, frugivore species, the microhabitat in 1-m radius, and whether they contained visible intact (i.e. no predated) *C. humilis* seeds. Though we could have missed the presence of seeds in largely buried feces, we would have detected any emerged seedling from such undetected seeds during our detailed monthly monitoring. Besides, to consider potential sites of seed dispersal by our target frugivores, we also recorded any feces that did not contain any seeds. To prevent trampling by ungulates, we isolated all feces containing *C. humilis* seeds with a bottom-open cubic wire mesh (10 ×10×9 cm) (Fig. A.2). We recorded the precise geographic coordinates of every dwarf palm individual in both study sites and entered them into a geographic information system using QGIS software (Fig. 1).

2.4. Spatial point pattern analyses

2.4.1. Univariate analysis of spatial clustering of mammal feces

To spatially characterize the observed distribution of mammal feces (all species together, seed predators [i.e. red deer and wild boar, grouped as ungulates], seed dispersers [i.e. badger and red fox together and separately], and feces with *C. humilis* seeds independently of mammal species), we used univariate Thomas cluster point processes. Specifically, we used four different summary functions: the pair-correlation function $g(r)$, the L-function $L(r)$, the spherical contact distribution $H_S(r)$, and the nearest neighbor distribution function $D(r)$ (Illian et al., 2008; Wiegand and Moloney, 2013). These functions provide together a good description of the potentially complex spatial structure of homogenous patterns (Wiegand et al., 2013). Specifically, the $g(r)$ and $L(r)$ can be calculated for the Thomas cluster point processes and are therefore traditionally used to fit their parameters (e.g. Diggle, 2013). Because the $g(r)$ is especially sensitive to clustering at small scales and the $L(r)$ is more sensitive to clustering at larger scales, their combined use yields an improved parameter fitting (Wiegand et al., 2009). However, both functions are usually not sufficient to characterize more complex spatial patterns and must be supplemented with functions that capture different types of spatial information such as the presence of gaps, isolated points or areas of low density of points (Wiegand et al., 2013). Thus, we used as additional summary functions the $H_S(r)$ and the $D(r)$. The $H_S(r)$ gives the proportion of 'test locations' that have at least one neighbor within distance r and therefore, characterizes the size of the 'holes' in the pattern (i.e. size of spots without plants). The $D(r)$ gives the proportion of woody plants that have at least one neighbor within distance r and characterizes the small-scale clustering in more detail (Illian et al., 2008; Wiegand et al., 2013).

We analyzed whether the four functions yielded a good agreement with the null model. Then, we constructed the simplest null model for the combinations of mammal feces specified above in each site and each seed dispersal season, as well as for the subset of feces with *C. humilis*

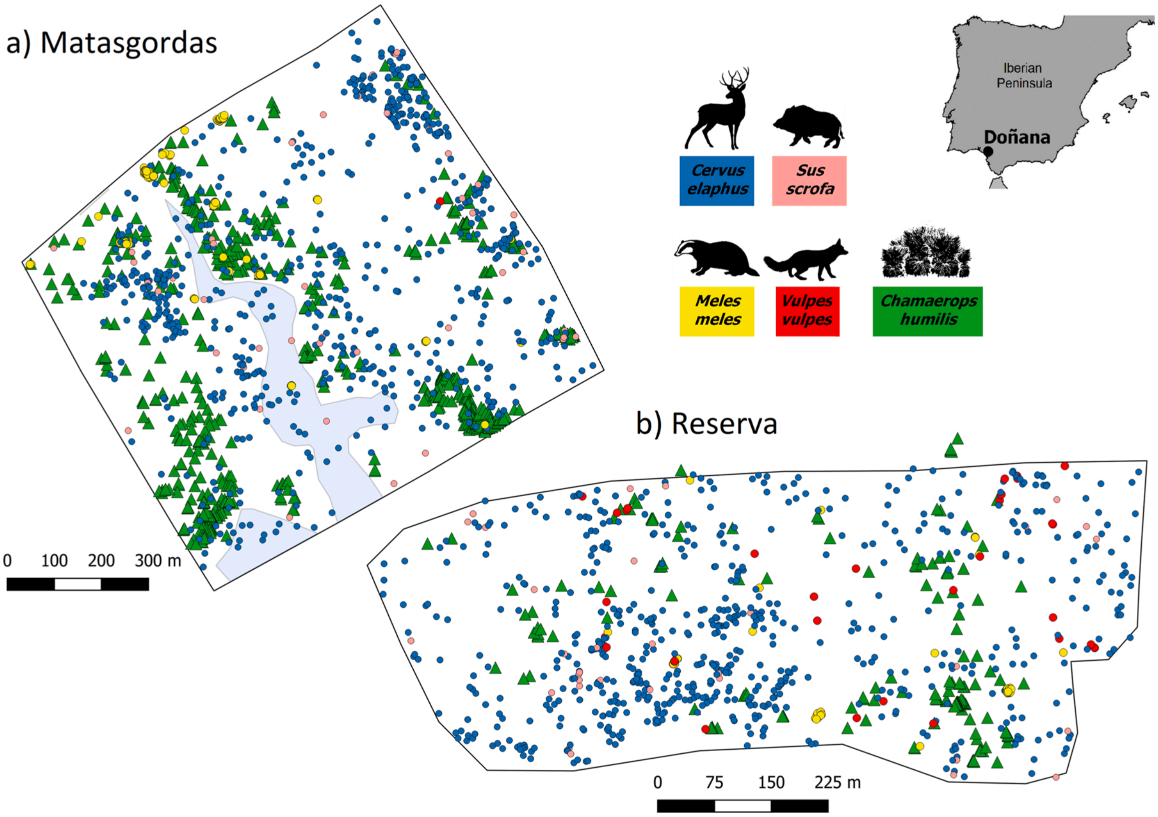

Fig. 1. Mammal feces (circles) and spatial distribution of adult individuals of the Mediterranean dwarf palm (green triangles; male and female plants) in (a) Matasgordas and (b) Reserva. Marshland in Matasgordas is represented in light blue. Location of Doñana National Park in Iberian Peninsula (SW Spain) is shown in the upper right corner.

seeds regardless of the frugivore species (Table A.1). The recommended and minimum number of points (i.e. feces) for these point processes is 100 (Wiegand et al., 2016; Żywiec et al., 2018). However, despite limited sample sizes, null models for badger in both sites and for red fox in Reserva fitted correctly. The complexity of spatial processes may increase from the simplest class of cluster processes with one critical scale of clustering up to the superposition of either a random component or a negative binomial component on a double-clustered component. Then, we selected the simplest point process that fitted all four target functions (see additional details in Appendix A).

(i) *Single-cluster process*: First, we tested a simple Thomas process which incorporates one critical scale of clustering. This point process consists of a number of randomly and independently distributed clusters.

(ii) *Double-cluster process*: This point process has two critical scales of clustering and the only difference is that the cluster centers are not randomly distributed but are assumed to follow a Thomas process with one critical scale of clustering.

(iii) *Double-cluster-isolation superposition*: Finally, we used a point process composed by a Thomas process with two critical scales of clustering and an independent superposition of an isolated pattern.

2.4.2. *Bivariate analysis of spatial association*

To quantify spatial associations (positive, negative, or neutral) of mammal feces and of mammal feces and adult dwarf palms in each study site (Table A.1), we used the bivariate pair-correlation function $g_{12}(r)$ (Wiegand and Moloney, 2013). Specifically, we analyzed whether there was spatial association between: (*i*) the feces (with and without seeds) in both seed dispersal seasons (i.e. 2017 vs. 2018); (*ii*) the accumulated feces (with and without *C. humilis* seeds) during both dispersal seasons pooled together (i.e. 2017 + 2018) and adult palms; and (*iii*) the accumulated feces with *C. humilis* seeds and adult palms. First, to quantify whether the feces are spatially associated between seed dispersal seasons, the feces of 2017 represent the spatial pattern 1 and the feces of 2018 represent the spatial pattern 2 for the bivariate pair correlation function $g_{12}(r)$. The spatial pattern 1 is a fixed pattern whereas the spatial pattern 2 moves according to the simplest null model fitted by Thomas cluster processes (Table 2). Thus, we can detect ecological patterns (e.g. consistency between dispersal seasons in areas used for defecation) through analyses of spatial association. Second, to quantify whether the accumulated feces are spatially associated with the spatial distribution of adult palms, the spatial pattern 1 is the observed distribution of adult palms, and the spatial pattern 2 are the accumulated feces. Like above, while adult palms represent a fixed pattern, the accumulated feces through both dispersal seasons move according to the simplest null model (Table 2). In this manner, we can assess whether the spatial patterns of defecation of different species of *C. humilis*' consumers (independently they disperse or not its seeds) are spatially associated with adult palms. Third, to quantify whether the accumulated feces with *C. humilis* seeds are spatially associated with the adult palms, the spatial patterns 1 and 2 are represented by the spatial distributions of adult palms and the *C. humilis* seed rain, respectively. Similarly, the observed distribution of adult palms is a fixed pattern and the feces with *C. humilis* seeds move according to the simplest null model fitted by the Thomas cluster process (Table 2). Thus, we can detect positive, negative, or neutral associations between the observed distribution of adult palms and the defecation patterns of *C. humilis*' dispersers. In all these analyses, if the bivariate pair correlation function $g_{12}(r)$ yields departures above the top or below the bottom simulation envelopes indicate higher (i.e. positive association) or lower (i.e. negative association) than expected spatial association of both specific spatial patterns, respectively. Observed values within the simulation envelopes indicate neutral

Table 2

Summary of the null models constructed for the spatial distribution of mammal feces (together and separately) in each study site (Matasgordas and Reserva) and each seed dispersal season (2017 and 2018). These null models were fitted with the Thomas cluster process (DC: double-clustered; SC: single-clustered). Note: N = total number of feces; N_{isol} = number of feces in isolated pattern; Pc = proportion of feces in isolated pattern; Pc^2= the square of Pc; Subscripts 1 and 2 indicate large and small cluster size, respectively; $A\rho_1$ = the number of large clusters in the study site of area A; $2\sigma_1$ (m) = the size of large clusters; $A\rho_2$ = the number of small clusters in the study site of area A; $2\sigma_2$ (m) = the size of small clusters; μ_1, μ_2 = average number of feces in one large-scale and one small-scale cluster, respectively; ρ_2/ρ_1 = average number of small clusters in one large clusters; σ_1/σ_2 = the size of large clusters relative to the size of small clusters. †Wild boar and red deer feces are grouped into 'ungulates'. ‡Feces with *Chamaerops humilis* seeds.

						Large clusters			Small clusters				
Matasgordas	Thomas process	N	N_{isol}	Pc	Pc^2	$A\rho_1$	$2\sigma_1$ (m)	μ_1	$A\rho_2$	$2\sigma_2$ (m)	μ_2	ρ_2/ρ_1	σ_1/σ_2
All mammal species 17 & 18	DC (ring = 3)	892	310	0.65	0.43	36.36	37.10	24.54	80.89	6.15	11.03	2.22	6.03
All mammal species 17	DC (ring = 3)	702	250	0.64	0.41	45.56	20.82	15.41	106.46	4.34	6.59	2.34	4.80
All mammal species 18	DC (ring = 3)	190	60	0.68	0.47	17.93	32.62	10.60	154.25	3.70	1.23	8.61	8.82
†Ungulates 17 & 18	DC (ring = 5)	716	225	0.69	0.47	24.37	40.32	29.38	1208.33	7.24	0.59	49.58	5.57
Ungulates 17	DC (ring = 5)	546	190	0.65	0.43	26.86	39.99	20.32	827.09	10.67	0.66	30.79	3.75
Ungulates 18	DC (ring = 5)	170	45	0.74	0.54	15.23	36.48	11.16	303.20	5.08	0.56	19.91	7.18
Badger 17 & 18	DC (ring = 3)	175	10	0.94	0.89	10.35	10.62	16.91	15.85	3.43	11.04	1.53	3.10
Badger 17	DC (ring = 3)	155	10	0.94	0.88	11.36	11.66	13.65	13.51	3.71	11.47	1.19	3.14
Badger 18	SC (ring = 3)	20	2	0.90	0.81	4.14	3.16	4.83	*None*	*None*	–	–	–
‡Feces with seeds 17 & 18	DC (ring = 3)	174	20	0.89	0.78	8.08	11.66	21.52	13.05	3.71	13.33	1.61	3.14
Reserva													
All mammal species 17 & 18	DC (ring = 3)	777	290	0.63	0.39	6.49	93.26	119.66	117.03	4.70	6.64	18.02	19.84
All mammal species 17	DC (ring = 3)	502	130	0.74	0.55	2.45	212.00	204.97	228.06	6.00	2.20	93.12	35.33
All mammal species 18	DC (ring = 3)	275	80	0.71	0.50	9.04	67.61	30.42	51.74	3.33	5.32	5.72	20.30
Ungulates 17 & 18	DC (ring = 5)	678	170	0.75	0.56	9.21	82.60	73.60	244.21	10.03	2.78	26.51	8.24
Ungulates 17	DC (ring = 5)	444	70	0.84	0.71	9.45	100.50	46.98	380.38	8.08	1.17	40.25	12.44
Ungulates 18	DC (ring = 5)	234	40	0.83	0.69	19.91	41.94	11.76	344.08	6.49	0.68	17.29	6.46
Badger + Red fox 17 & 18	SC (ring = 3)	99	25	0.75	0.56	4.37	3.52	22.66	*None*	*None*	–	–	–
Badger + Red fox 17	SC (ring = 3)	58	22	0.62	0.39	6.05	3.84	9.59	*None*	*None*	–	–	–
Badger + Red fox 18	SC (ring = 3)	41	9	0.78	0.61	1.53	3.11	26.82	*None*	*None*	–	–	–
Badger 17 & 18	SC (ring = 3)	68	12	0.82	0.68	2.51	3.50	27.10	*None*	*None*	–	–	–
Badger 17	SC (ring = 3)	33	10	0.70	0.49	2.67	3.63	12.35	*None*	*None*	–	–	–
Badger 18	SC (ring = 3)	35	2	0.94	0.89	1.62	3.10	21.63	*None*	*None*	–	–	–
Red fox 17 & 18	DC (ring = 7)	31	–	–	–	37.73	20.32	0.82	106.90	4.39	0.29	2.83	4.63
Red fox 17	DC (ring = 7)	25	–	–	–	15.85	69.33	1.58	54.85	4.97	0.46	3.46	13.95
Feces with seeds 17 & 18	SC (ring = 3)	48	15	0.69	0.47	3.20	3.10	15.00	*None*	*None*	–	–	–

association.

2.4.3. *Statistical details of spatial analyses*

To test the fit of data with the point process models, we conducted 199 simulations of the fitted point processes and estimated envelopes with an approximate error rate of α = 0.05 (Stoyan and Stoyan, 1994), which are the fifth lowest and highest values of the summary statistics of the simulated point process. To test the fitted univariate and bivariate cluster processes and departures from the null model, we used simulation envelopes and goodness-of-fit test (see additional details in Appendix A). Observed values above the top or below the bottom simulation envelopes indicate higher or lower than expected spatial association, respectively. Observed values within the simulation envelopes indicate a level of spatial association compatible with the stochasticity of the point process model. For all point pattern analyses, we used the grid-based software Programita (Wiegand and Moloney, 2013).

2.5. *Dispersal kernels analyses*

To estimate whether seedling tended to survive more often close or away from adult mother plants, we inferred minimum dispersal distances (i.e. linear distance to the nearest adult reproductive female palm) for emerged and surviving *C. humilis* seedlings within mammal feces. In other words, we estimated 'basic' and 'effective' dispersal kernels of emerged and surviving seedlings, respectively. To this aim, first, we monthly monitored all excluded feces from January 2018 to December 2019 (i.e. the end of the study) in each site. We counted emerged seedlings and marked them with colored plastic straws identifying their month of emergence (Fig. A.3). Seedling mortality was also recorded monthly and most often was due to desiccation (generally during summer), although some apparently desiccated seedlings (32.8%; N = 1604) resprouted after the first fall rains. Then, we calculated the accumulated number of both emerged and surviving *C. humilis* seedlings of each studied cohort (i.e. dispersed in 2017 and 2018) by the end of the study (December 2019). Second, we calculated (using QGIS software) a distance matrix comprised of the linear distance from each seedling to its nearest female dwarf palm. Then, we fitted probability density functions (Normal, *t*-Student, log-Normal, Weibull, exponential, gamma and Cauchy) to describe mathematically dispersal distributions. We estimated their parameters using maximum-likelihood estimation. Because empirical distance distributions showed multiple peaks, we fitted mixture distributions following the method implemented by González-Varo et al. (2013). Specifically, we partitioned the data into unimodal distributions based on visual inspection of distance intervals. Then, we fitted the probability density functions to each of these data partitions separately (i.e. each peak or distance interval). Finally, we fitted mixture distributions using the parameters estimated from best-fitting unimodal distributions as starting points. We used Akaike's Information Criterion (AIC; Burnham et al., 2011) for model selection of unimodal distributions, while in the multimodal distributions, we selected the best model by comparing AIC of unimodal and multimodal density functions. We fitted all dispersal kernels using R packages *fitdistrplus* (Delignette-Muller et al., 2011), *bblme* (Bolker and Bolker, 2020), and *emdbook* (Bolker, 2011).

2.6. *Assessment of Janzen-Connell and facilitative effects*

To assess potential Janzen-Connell and/or facilitative effects, we related seedling survival to the distance to the nearest female palm by fitting logistic regressions (alive and dead seedlings were coded as 1 and 0, respectively). Additionally, we calculated the percentage of surviving seedlings by the end of the study for intervals of increasing distance from the nearest female palm (i.e. 0 – 25 m, 25 – 50 m, 50 – 75 m, and 75 – 100 m).

3. Results

3.1. *The spatial pattern of mammal feces and their spatial association between dispersal seasons*

We found species and site-specific differences in the spatial distribution of mammal feces (Table 2). Overall, the spatial distribution of feces was described by either single- or double-clustered patterns with an isolated component pattern. The summary functions showed simultaneous good agreement for almost all species, and departures of observed values from model-predicted ones were always small (Table A.2).

Feces (with and without *C. humilis* seeds; Table 3) of all mammal species (together and separately) were positively associated between seed dispersal seasons in Matasgordas (Fig. A.4), with the spatial scale of such association being species-specific. For ungulates (i.e. red deer and wild boar), the level of spatial association (i.e. the observed values of g_{12}(r)) was between 1.5 and 3.8 times greater than the expected ones, with the scale of positive seasonal association up to 50 m. For badger feces the observed values of g_{12}(r) were 17.2- and 561.9-times greater than the expected ones for scales up to 14 m.

In Reserva, we also found species-specific differences in the spatial scale and the strength of mammal feces seasonal association (Fig. A.5). Thus, considering ungulates feces, the scale of association was up to 50 m, with observed values of g_{12}(r) between 1.4- and 2.6-times greater than the expected ones. As above, we found strong positive spatial seasonal association of badger feces at short scales. Specifically, badger feces from both seed dispersal seasons were associated up to 8 m, with the observed values of g_{12}(r) ranging between 5.1- and 2666.6-times greater than expected. When badger and red fox feces were analyzed together, their seasonal association (also for scales up to 8 m) was between 10.6 and 166.9 times greater than the expected.

3.2. *Spatial association between mammal feces and adult dwarf palms*

There were marked site-specific differences in the spatial associations between the feces (accumulated during both dispersal seasons) and the distribution of adult palms (Fig. 2). In Matasgordas, the fecal marking behavior of badgers yielded strong positive spatial associations ($P < 0.03$) at short scales (Fig. 2c). Conversely, ungulate feces (almost all without *C. humilis* seeds; Table 3) did not show significant spatial association with adult dwarf palms (Rank = 149, $P = 0.26$; Fig. 2b). In Reserva, we found no significant spatial associations (Rank $\geq$ 97, $P \geq 0.15$) between the accumulated feces of all mammal species and the distribution of adult palms (Fig. 2d-h). Interestingly, we found some significant evidence of positive spatial associations (Rank $\geq$ 196; $P \leq 0.03$) between badger feces (either including red fox feces or not) and adult dwarf palms at large scales (45 – 50 m; Fig. 2f and g).

3.3. *Spatial association between feces with C. humilis seeds and adult dwarf palms*

When considering only the subset of mammal feces containing *C. humilis* seeds, we found site-specific differences for their spatial association with adult dwarf palms. In Matasgordas, there was a strong positive spatial association up to 6 m, with observed values of g_{12}(r) between 6.0 and 28.2 times greater than expected (Fig. 3a). In other words, feces with *C. humilis* seeds ($N = 174$; $n_{\text{badger}} = 170$, $n_{\text{wild boar}} = 3$, $n_{\text{red fox}} = 1$; Table 3) were more spatially aggregated with adult palms at short scales than expected. In contrast, in Reserva, we only found slight but significant positive associations between 45 and 50 m (Rank = 192, $P = 0.045$), with observed values of g_{12}(r) between four and five times greater than expected (Fig. 3b). That is, feces with *C. humilis* seeds ($N = 48$; $n_{\text{badger}} = 41$, $n_{\text{red fox}} = 7$; Table 3) were spatially aggregated with adult palms at a larger scale than in Matasgordas.

3.4. *Relationship between dispersal distances and seedling emergence and survival*

In Matasgordas, we inferred minimum dispersal distances (i.e. from the nearest dwarf palm female) for the overall number of emerged ($N = 1292$) and surviving ($N = 325$) *C. humilis* seedlings within

Table 3

Sample sizes and other descriptive information for each mammal's species, seed dispersal season, and study site. Note: TNF = total number of feces; TNFnSD = total number of feces without seeds; TNFwSD = total number of feces with seeds; TNFwSL = total number of feces with seedlings; TNESL = total number of emerged seedlings; NESLF = mean number (± SE) of emerged seedlings per feces; TNSSL = total number of surviving seedlings; NSSLF = mean number (± SE) of surviving seedlings per feces; DFnSD = mean distance (m) (± SE) of feces without seeds to the nearest female dwarf palm; DFwSD = mean distance (m) (± SE) of feces with seeds to the nearest female dwarf palm; DFwSL = mean distance (m) (± SE) of feces with seedlings to the nearest female dwarf palm.

Study site	Season	Mammal species	TNF	TNFnSD	TNFwSD	TNFwSL	TNESL	NESLF	TNSSL	NSSLF	DFnSD	DFwSD	DFwSL
Matasgordas	2017	*Cervus elaphus*	511	511	0	0	0	0	0	0	57.2 ± 2.5	0	0
		Sus scrofa	35	32	3	0	0	0	0	0	53.7 ± 10.4	51.6 ± 28.3	0
		Meles meles	155	0	155	97	1279	13.2 ± 1.9	320	6.4 ± 0.9	0	24.8 ± 2.0	25.7 ± 2.6
		Vulpes vulpes	1	0	1	0	0	0	0	0	0	12.4	0
	2018	*Cervus elaphus*	161	161	0	0	0	0	0	0	68.8 ± 4.9	0	0
		Sus scrofa	9	9	0	0	0	0	0	0	63.3 ± 16.1	0	0
		Meles meles	20	5	15	4	13	3.3 ± 0.5	5	1.7 ± 0.3	43.0 ± 13.1	25.4 ± 7.5	5.8 ± 2.2
		Vulpes vulpes	0	0	0	0	0	0	0	0	0	0	0
Reserva	2017	*Cervus elaphus*	427	427	0	0	0	0	0	0	52.7 ± 1.4	0	0
		Sus scrofa	17	17	0	0	0	0	0	0	46.6 ± 7.7	0	0
		Meles meles	33	2	31	21	306	14.6 ± 2.5	54	4.2 ± 1.4	25.8 ± 7.4	30.3 ± 3.3	31.1 ± 4.3
		Vulpes vulpes	25	20	5	2	3	1.5 ± 0.5	0	0	58.4 ± 6.6	29.4 ± 10.4	15.4 ± 2.6
	2018	*Cervus elaphus*	216	216	0	0	0	0	0	0	53.6 ± 2.0	0	0
		Sus scrofa	18	18	0	0	0	0	0	0	55.7 ± 5.2	0	0
		Meles meles	35	25	10	2	3	1.5 ± 0.5	0	0	27.5 ± 3.0	30.4 ± 7.0	32.7 ± 0.1
		Vulpes vulpes	6	4	2	0	0	0	0	0	34.7 ± 12.9	3.1 ± 0.3	0

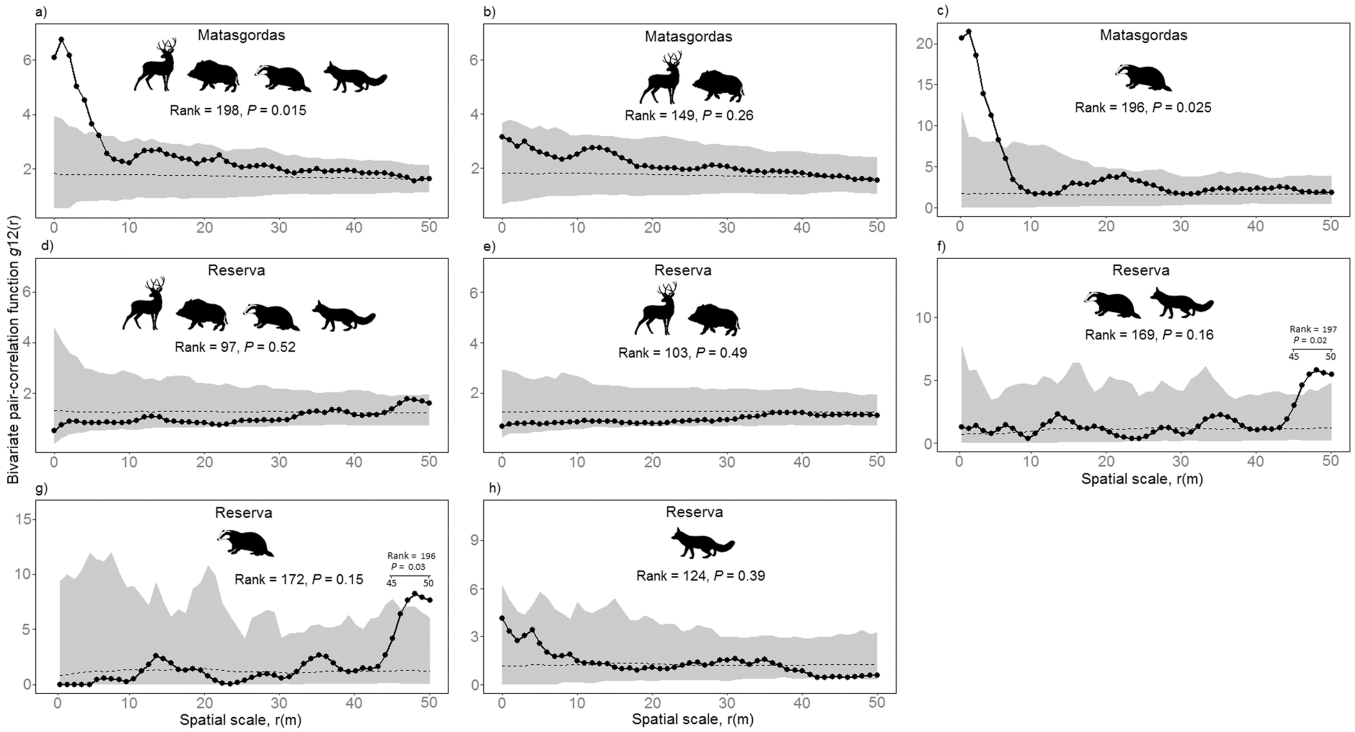

Fig. 2. Bivariate analyses between mammal feces (combined and separately) and the spatial distribution of adult palms in (a-c) Matasgordas and (d-h) Reserva. Shown for each summary function is the bivariate pair-correlation function g_{12}(r) of the data (dotted black line), the expected function of the null model (dashed line), and the corresponding simulation envelopes (grey area; the 5th lowest and highest values for each summary function created by 199 simulations of the null model).

mammals' feces (Table 3). The number of emerged seedlings per fecal sample ranged from 1 to 121 seedlings (Table 3). We estimated an average minimum dispersal distance of 22.4 ± 0.6 m (median = 15.2 m; range = 0.4 – 84.4 m) (Table 3; Fig. 4a). The basic dispersal kernel for emerged seedlings was characterized by the presence of several peaks (Table A.3; Fig. A.6). The range of surviving seedlings per fecal sample by the end of the study was between 1 and 26 seedlings (Table 3). We estimated an average minimum dispersal distance of 15.4 ± 0.7 m (median = 14.5 m; range = 0.4 – 79.7 m) (Table 3; Fig. 4c). The effective dispersal kernel for the accumulated surviving seedlings was also characterized by the presence of several peaks (Table A.3; Fig. A.7). The percentage of emerged seedlings that survived by the end of the study was much higher for short-distance dispersal events (being 29.1%, 17.3%, 15.9%, and 0.08%, for the intervals 0 – 25 m, 25 – 50 m, 50 – 75 m, and 75 – 100 m, respectively). The probability of seedling survival significantly decreased as the distance to the nearest female palm increased ($\chi^2 = 0.004$, $P < 0.001$; Fig. 5).

In Reserva, there emerged a total of 312 *C. humilis* seedlings, ranging from 1 to 45 seedlings per fecal sample (Table 3). The estimated average minimum dispersal distance of emerged seedlings was 29.01 ± 1.06 m (median = 33.08 m; range = 6.04 – 91.05 m) (Table 3; Fig. 4b). As above, the basic dispersal kernel for the accumulated emerged seedlings was characterized by the presence of several peaks (Table A.3; Fig. A.8). Overall, 54 seedlings survived by the end of the study, with 1–20 surviving seedling per fecal sample (Table 3). The average minimum dispersal distance of surviving seedlings was 35.26 ± 2.85 m (median = 35.51 m; range = 6.04 – 91.05 m) (Table 3; Fig. 4d). The effective dispersal kernel for the accumulated surviving seedlings was also characterized by the presence of several peaks (Table A.3; Fig. A.9). In contrast to findings from Matasgordas, the percentage of surviving seedlings was higher for larger distance dispersal events (being 13.5%, 12.4%, 32.3%, 33.3%, and for the intervals 0 – 25 m, 25 – 50 m, 50 – 75 m, and 75 – 100 m, respectively). The greater the distance to the nearest female palm, the greater the probability of seedling survival ($\chi^2 = 2.65$, $P < 0.01$; Fig. 5).

4. Discussion

We found strong differences between study sites in the strength and scale of spatial associations of mammal feces with adult dwarf palms. Further, there was some site-specific evidence of both Janzen-Connell and facilitative effects as indicated by variation in the percentage of seedling survival with dispersal distance. Interestingly, the relationship between seedling survival and dispersal distance was negative in one study site (Matasgordas) while positive in the other one (Reserva), suggesting context-dependency in the outcome of the interaction between *Chamaerops humilis* and its seed dispersers (Perea et al., 2013). Altogether, our results help us to improve the comprehension of central ecological processes in the natural (re)colonization of Mediterranean human-altered ecosystems (e.g. old-fields) such as seed dispersal, and the underlying mechanisms driving spatial and demographic patterns.

4.1. Spatial associations between mammal feces and between mammal feces and adult dwarf palms

We revealed strong positive spatial associations of mammal feces from both monitored seed dispersal seasons. Thus, we elucidated the potential role of frugivorous mammals in plant (re)colonization of vacant human-disturbed areas by promoting a continued seed arrival through time (Howe and Miriti, 2000; Beckman and Rogers, 2013). Likely, the sustained use of habitat across both dispersal seasons by our target frugivores, independently of whether they disperse *C. humilis* seeds or not, generated these spatial patterns of positive association. Importantly, we detected a much lower fecal deposition of some mammal species during the dispersal season 2017 as compared to 2018 (e.g. red deer in both study sites, red fox in Reserva, or badger in Matasgordas). These changes might be partially due to local displacements of mammals to other habitats (e.g. pine forests) within study areas which

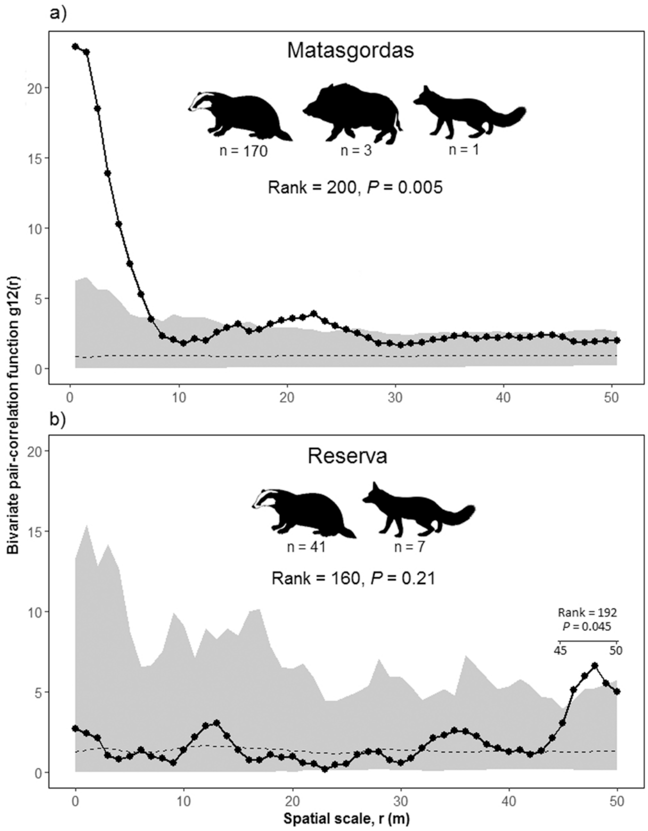

Fig. 3. Bivariate analyses between mammal feces with *Chamaerops humilis* seeds and the spatial distribution of adult palms in (a) Matasgordas and (b) Reserva. Shown for each summary function is the bivariate pair-correlation function $g_{12}(r)$ of the data (dotted black line), the expected function of the null model (dashed line), and the corresponding simulation envelopes (grey area; the 5th lowest and highest values for each summary function created by 199 simulations of the null model).

could relate to the observed decrease in *C. humilis* fruiting (Authors, *unpublished data*) and/or to an increase in availability of other fleshy-fruited species during the second dispersal season (e.g. *R. ulmifolius, P. bourgaeana*; Garrote et al., 2018). Despite this inter-annual variation, the important role of these frugivores as seed dispersers relates not only with *C. humilis* but also with the intense and consistent seed dispersal of multiple woody and herb species (Perea

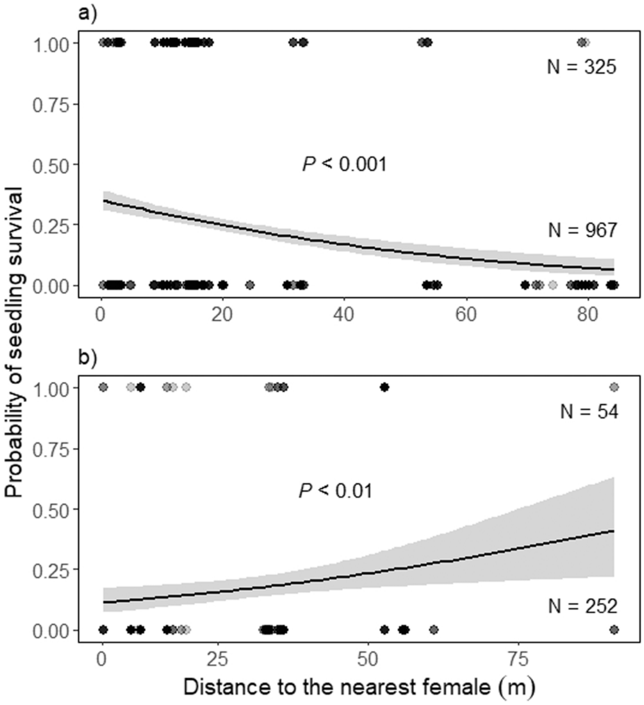

Fig. 5. Logistic regressions for the probability of *Chamaerops humilis* seedling survival with respect to the distance of feces to the nearest female palm in (a) Matasgordas and (b) Reserva. Dots represent (1) living or (0) dead seedlings. Grey areas represent 95% confidence intervals.

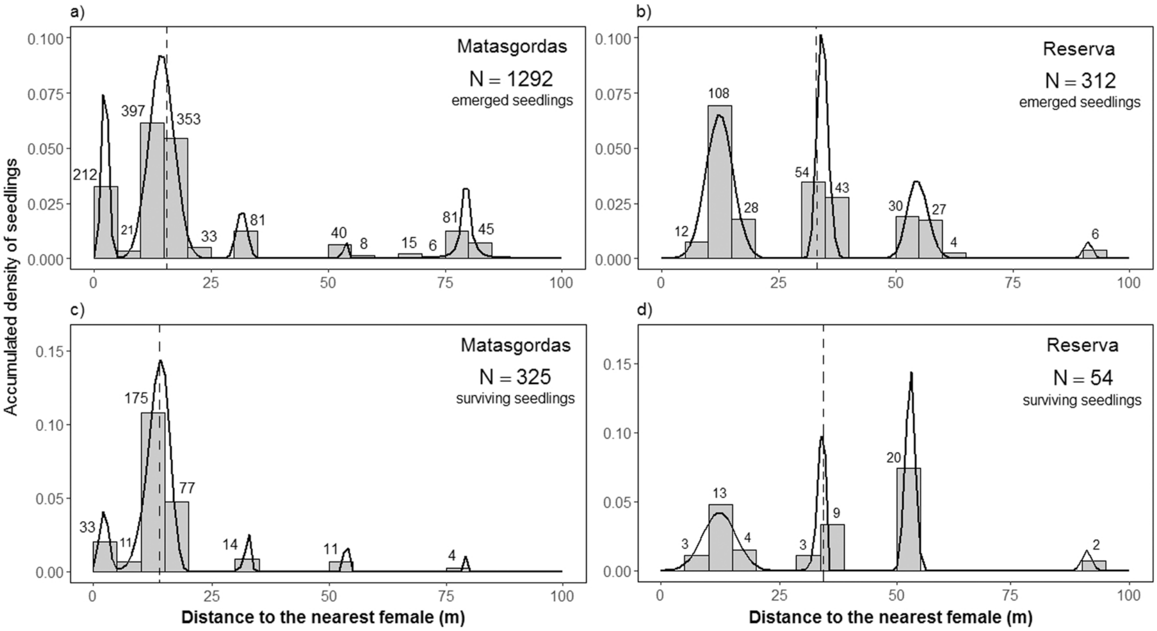

Fig. 4. Kernels of the accumulated number of both emerged (basic dispersal kernel) and surviving *Chamaerops humilis* seedlings (effective dispersal kernel) in (a, c) Matasgordas and (b, d) Reserva. Numbers above bars represent observed frequency distributions; solid lines represent the best-fitting probability density functions, and dashed lines represent the median distance to the nearest dwarf palm female (i.e. the minimum seed dispersal distance).

et al., 2013; Loayza et al., 2020; Selwyn et al., 2020).

The overall aggregation pattern between dispersal seasons was consistent between study sites. The differences between study sites in the number of feces from different mammal species were likely due to contrasting mammal abundances in each area. For instance, we only found a single red fox fecal sample in Matasgordas during both dispersal seasons. In this area, the red fox population has been historically reduced by human-related causes (e.g. illegal poaching, road-kill; Fedriani et al., 2020). Besides, we cannot rule out the possibility of predation of some red foxes by Iberian lynxes in this study site. Thus, we apparently detected the virtual loss of an important ecosystem service (i.e. seed dispersal) provided by red foxes, with potential detrimental effects on plant recruitment, establishment, and distribution (Caughlin et al., 2015; Pires et al., 2018).

The spatial association between feces and adult dwarf palms varied in sign and strength depending on the mammal species and the study site. Nonetheless, our results clearly emphasize the important role of badgers in the (re)colonization of Mediterranean human-altered landscapes by reinforcing those habitat patches dominated by a keystone pioneer palm. Moreover, the well-known role of badgers as legitimate seed dispersers (Fedriani and Delibes, 2008; López-Bao and González-Varo, 2011), together with the strong facilitative effects exerted by the dwarf palm on the seedling survival and establishment of several late-successional species (Garrote et al., 2019, 2021), could trigger crucial nucleation processes for the improvement of natural (re) colonization (Pausas et al., 2006; Holl et al., 2020). Finally, we did not observe significant spatial associations between ungulate feces (i.e. red deer and wild boar) and the spatial distribution of adult dwarf palms. Even though both red deer and wild boar usually browse and eat dwarf palm fruits (Selwyn et al., 2020), they do not show fecal marking of their home ranges (in contrast with carnivores) but they usually defecate as they walk and therefore, such spatial associations are less probable. Further, we found they practically did not disperse any *C. humilis* seed in their feces given that they mainly act as seed predators. Nonetheless, these wild and some domestic (e.g. horse, cow) ungulate species often disperse seeds of a large number of woody and herb species (Fedriani and Delibes, 2008; Suárez-Esteban et al., 2013; Petersen and Bruun, 2019). Therefore, additional studies are required to fully disentangle the role of both wild and domestic ungulates as seed dispersers in human-altered habitats (e.g. via regurgitation from the cud; Castañeda et al., 2018).

4.2. Seed dispersal was spatially associated with adult dwarf palms

Despite some differences between sites in the scale and strength of spatial associations between feces with *C. humilis* seeds and adult dwarf palms, there were also some invariant patterns. Thus, in both study sites, badgers were the main animal responsible for the detected spatial patterns. Although we focused on *C. humilis* seeds due to the ecological importance of this keystone palm (Muñoz-Gallego et al., 2019; Garrote et al., 2019, 2021; Selwyn et al., 2020; González et al. *Unpublished results*), badgers (and to a lesser extent red foxes and wild boar) often disperse numerous late-successional plant species. Indeed, we also detected seeds of fleshy-fruited species such as *P. bourgaeana*, *O. europaea* var. *sylvestris*, and *R. ulmifolius* in mammal feces (Fedriani and Delibes, 2008). Importantly, the fact that they can disperse seeds in a spatially contagious fashion (Fedriani and Wiegand, 2014) may have both positive (e.g. associational resistance) and negative effects (e.g. associational susceptibility) (Barbosa et al., 2009) not only in the seed stage but also in subsequent plant life stages such as seedlings and saplings (Wang and Smith, 2002).

Regarding the differences between both sites, the fecal marking behavior of badgers (i.e. latrines) determined the spatial associations with adult dwarf palms. On the one hand, the strong spatial aggregation of feces with adult dwarf palms in Matasgordas was likely due to badgers often placing their latrines close to their main seasonal feeding resources (i.e. *C. humilis* fruits). Thus, badgers could reinforce habitat patches dominated by this keystone pioneer palm. On the other hand, badger latrines in Reserva were farther from adult dwarf palms than in Matasgordas. Therefore, in Reserva badgers have a greater potential to eventually create new dwarf palm patches. Nonetheless, the several peaks of dispersal kernels indicate that badgers in both study sites (by delivering feces in latrines located in a range of distances from adult dwarf palms) can potentially either reinforce existing *C. humilis* patches or create new ones. Interestingly, badgers usually deflesh fruits during their partial digestion and then, most often deposit their feces with seeds in small holes they excavate in the sandy substrate (about 10 cm deep) and bury them shallowly with loose sand (Fedriani and Delibes, 2011). Likely, that burial increases seed survival by preventing attacks by invertebrates and by ameliorating microclimatic conditions. Most (83% and 75% in Reserva and Matasgordas, respectively) *C. humilis* seedlings that emerged from badger feces died by the end of the study. This is, however, a relatively high seedling survival since unburied *C. humilis* seeds rarely thrive in Doñana (Authors, *unpublished data*).

Seedling emergence and survival can also be affected in different ways by the presence of adult conspecifics through either Janzen-Connell (*sensu* Connell, 1971; Janzen, 1970) or facilitative effects (*sensu* Callaway, 2007). Indeed, we found evidences of both facilitative and Janzen-Connell effects depending on the study site. Thus, in Matasgordas, the greater proportion of surviving seedlings near to adult plants suggest facilitative effects (e.g. Garrote et al., 2022). By contrast, in Reserva, the greater seedling survival far from adult plants suggest Janzen-Connell effects. Microgeographic variation in the Doñana area in post-dispersal seed predation by beetles and rodents (Rodríguez et al., 2014; Garrote et al., 2022), sapling herbivory by ungulates (Castilla et al., 2019), or even trampling by livestock could contribute to the detected between site differences. Field experiments must be designed specifically to identify the causes underlying the change between study sites in the type of effects. Finally, in a stressful environment such as the Mediterranean basin (Pugnaire and Valladares, 2007; Morán-Ordóñez et al., 2021), the suitability of microhabitat where seeds arrive is critical for seedling survival and establishment (Schupp, 2007; García-Cervigón et al., 2018). Generally, the most suitable microhabitat where plant species such as *C. humilis, P. bourgaeana,* or *Q. suber* in Doñana reach the greatest recruitment rates is the Mediterranean scrubland, although occasionally some species such as *C. humilis* can establish in open pasturelands. Indeed, in Matasgordas, there was a positive correlation between the percentage of microhabitat (1-m radius) occupied by shrubs around the mammal feces and the proportion of emerged seedlings that survived by the end of the study (Fig. A.10). This correlation was not found in Reserva, likely because there was not much variation in the microhabitat of seed deposition (i.e. 80% of feces were deposited in open microhabitat without shrubs).

4.3. Concluding remarks

We disentangled the spatial patterns of the seed rain of a pioneer palm with a keystone role in the (re)colonization of Mediterranean human-altered landscapes. We emphasize the central role of Eurasian badgers over other frugivorous mammals (e.g. red fox, ungulates) by dispersing large number of seeds during (re)colonization events. The local virtual loss of seed dispersal service provided by red foxes highlights the negative consequences of recent human-driven defaunation. Finally, we stress the importance of context-dependency (e.g. dispersal seasons, sites, frugivores species) in understanding the underlying mechanisms and processes driving the early (re)colonization of human-impacted habitats.

CRediT authorship contribution statement

Pedro J. Garrote: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – Original Draft, Writing – Review & Editing, Visualization. **Antonio R. Castilla:** Methodology, Investigation, Writing – Review & Editing. **Jose M. Fedriani:** Conceptualization, Methodology, Investigation, Writing – Review & Editing, Supervision, Project administration, Funding acquisition.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2022.125685.

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