



Examining the spatiotemporal variation of genetic diversity and genetic rarity in the natural plant recolonization of human-altered areas

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Abstract

The spatiotemporal genetic variation at early plant life stages may substantially affect the natural recolonization of human-altered areas, which is crucial to understand plant and habitat conservation. In animal-dispersed plants, dispersers' behavior may critically drive the distribution of genetic variation. Here, we examine how genetic rarity is spatially and temporally structured in seedlings of a keystone pioneer palm (*Chamaerops humilis*) and how the variation of genetic rarity could ultimately affect plant recruitment. We intensively monitored the seed rain mediated by two medium-sized carnivores during two consecutive seasons in a Mediterranean human-altered area. We genotyped 143 out of 309 detected seedlings using 12 microsatellite markers. We found that seedlings emerging from carnivore-dispersed seeds showed moderate to high levels of genetic diversity and no evidence of inbreeding. We found inflated kinship among seedlings that emerged from seeds within a single carnivore fecal sample, but a dilution of such FSGS at larger spatial scales (e.g. latrine). Seedlings showed a significant genetic sub-structure and the sibling relationships varied depending on the spatial scale. Rare genotypes arrived slightly later throughout the dispersal season and tended to be spatially isolated. However, genetic rarity was not a significant predictor by itself which indicates that, at least, its influence on seedling survival was smaller than other spatiotemporal factors. Our results suggest strong *C. humilis* resilience to genetic bottlenecks due to human disturbances. We highlight the study of plant-animal interactions from a genetic perspective since it provides crucial information for plant conservation and the recovery of genetic plant resilience.

Keywords Seed dispersal · Mediterranean human-altered areas · *Chamaerops humilis* · Pioneer plant · Fine-scale spatial genetic structure · Kinship · Seedling recruitment.

Introduction

The understanding of ecological processes driving the natural recolonization of human-altered areas is fundamental for the conservation of sensitive, endangered, and keystone species as well as for their ecosystem services (Egoh et al. 2007; Turner et al. 2007). In particular, seed dispersal is one of the most critical processes during recolonization as it ensures seed arrival to these altered areas (e.g. Escribano-Ávila et al. 2014; Cancio et al. 2017; Martínez-Baroja et al. 2019). Interestingly, the genetic composition of recruits may substantially affect recolonization fate. For instance, the genetic variation of recruits will ultimately influence future fine-scale spatial genetic structure (FSGS, hereafter) and can potentially impact individuals' reproductive success (Choo et al. 2012; Castilla et al. 2019). Similarly, recent studies have demonstrated that seedlings' genetic rarity

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(*sensu* Browne and Karubian 2016) affects their survival (Browne and Karubian 2018; Tito de Morais et al. 2020). However, few studies have examined how genetic variation across space and over time of naturally established seedlings is generated within human-altered areas and its potential consequences on plant recruitment (Gelmi-Candusso et al. 2017; Aguilar et al. 2019; but see Santos et al. 2016; Ismail et al. 2017). Therefore, comprehending how genetic variation may influence the fate of natural recolonization may be central for plant biodiversity conservation, especially in a quickly changing environment (Frankham et al. 2010; Kramer and Havens 2009; Kardos et al. 2021).

In animal-dispersed plants, dispersers' behavior can affect the spatial genetic structure of recolonizing plant populations (Jordano 2010; García and Grivet 2011). For instance, animal mobility can critically influence the intensity and shape of seed rain in target areas. In this regard, some studies have shown that large- and medium-sized mammals are highly mobile and play influential roles in the recolonizing human-altered areas by facilitating long-distance dispersal (e.g. Escribano-Ávila et al. 2014; Tsunamoto et al. 2020; but see Gamba and Muchhala 2020). Usually, frugivorous mammals may differ in their relative abundance, mobility, level of frugivory and fecal marking behavior (Fragoso and Huffman 2000; Fedriani and Wiegand 2014; Sakamoto and Takatsuki 2015). In particular, species defecating in latrines (i.e. set of several feces aggregated at scales of a few meters) may yield disproportionate seed clumps with potential genetic implications. For instance, recurrent mammal seed dispersal into latrines could dilute the FSGS of populations due to the genetic admixture (Vekemans and Hardy 2004; Giombini et al. 2016; Browne et al. 2018). Additionally, the study of sibling relationships among seedlings may be relevant for understanding the spatial structure of genetic variation in recolonizing plant populations. Interestingly, whether and how disperser species-specific patterns of seed deposition (e.g. latrines) affect the genetic makeup of seedlings has seldom been explored. This information can assist in detecting hotspots where genetic kinship may be inflated and in unmasking the sibling relationships over time and space, prompting the potential implementation of actions to alleviate inbreeding (e.g. translocation of particular genotypes; Weeks et al. 2011).

From a temporal perspective, the way in which the genetic composition of seed rain varies through dispersal season has been scarcely analyzed, probably because it requires time-consuming field monitoring. Given that the genetic makeup of seedlings can affect their emergence and survival (e.g. Fedriani et al. 2019), it is important to identify the timing when potential successful genotypes tend to reach recolonizing populations. Although a number of recent studies have found that genetically rare seedlings can impact plant recruitment (Browne and Karubian 2016, 2018; Tito

de Morais et al. 2020), the timing of rare seedlings' arrival remains unexplored. For instance, it may be possible that rare genotypes arrive (via seed dispersers) from other plant populations when fruit abundance is low in the local population. In other words, it would be expectable that out of the fruiting peak (e.g. early and/or late during seed dispersal season), dispersers move and forage further away, which may have the potential to introduce rare genotypes into the population. Under this scenario, identifying the temporal variation of seedlings' genetic makeup and its potential consequences on demographic processes such as seedling emergence, survival and recruitment may provide critical information for plant conservation.

Here, we quantify the genetic diversity and FSGS of naturally established seedlings and explore how the spatiotemporal structure of genetic rarity can affect seedling survival and, eventually, plant recruitment in human-altered habitats. To this end, we intensively monitored the seed rain of the pioneer Mediterranean dwarf palm (*Chamaerops humilis*, Arecaceae) during two consecutive dispersal seasons. We focused on a historically human-altered area (the Doñana National Park, SW Spain), where this dioecious palm is mainly dispersed by Eurasian badgers (*Meles meles*) and, to a lesser extent, by red foxes (*Vulpes vulpes*) (Fedriani and Delibes 2011; Selwyn et al. 2020). These medium-sized carnivores are highly mobile, able to cover several kilometers daily across their large home ranges (López-Martín 2017; Virgós 2017).

We hypothesize that seed dispersal by both carnivore species may impose some FSGS on *C. humilis* populations and that such genetic structure may have significant consequences on early demographic processes. This trend may be particularly marked for badgers due to their recurrent use of latrines and the potential higher contribution to seed rain regarding red foxes (Fedriani and Wiegand 2014; Garrote et al. 2022). Specifically, we predict: (i) Based on the high mobility of seed dispersers, considerable genetic diversity and the potential absence of inbreeding due to the levels of genetic diversity and admixture observed within local adults of *C. humilis* (*unpublished data*): We also expect (ii) positive FSGS at short spatial scales, (iii) a greater proportion of full- and half-sibs than non-sib seedlings within dispersers feces, and (iv) a greater proportion of non-sibs than full- and half-sibs within latrines. These predictions were based on the fecal marking behavior of badgers (i.e. latrines) and its potential consequences on sibling relationships at several hierarchical spatial scales. At start and end of dispersal season, the lower availability of fruiting palms may lead to dispersers foraging wider areas, increasing the odds for the arrival of rare genotypes earlier and/or later than at the local fruiting peak. Therefore, we expect (v) genetically rarer seedlings arrive at seed start and end of dispersal season due to lower availability of fruiting palms in the local site.

Finally, we expect (*vi*) that more rare genotypes will have higher survival.

Materials and methods

Study area and species

Chamaerops humilis is an endemic of the western Mediterranean basin (Guzmán et al. 2017). This pioneer palm plays a keystone role in the natural recolonization of human-altered areas by triggering positive spatial associations with multiple woody plant species (Garrote et al. 2021) and offering important feeding resources to a wide mammal assemblage (Muñoz-Gallego et al. 2019; Selwyn et al. 2020). The species is dioecious, with male and female plants coexisting within populations. Flowering occurs predominantly in spring (March–May). It exhibits a nursery-pollination system involving the specialist weevil *Derelomus chamaeropsis* (Curculionidae) (Anstett 1999; Dufaÿ and Anstett 2004) and the beetle *Meligethinus pallidulus* (Nitidulidae) (García et al. 2018). Fruits are polydrupes comprised of one to three drupes attached to dense infructescences of up to 30 cm long (7–120 fruits per infructescence; Selwyn et al. 2020; Fig. S1). Fruits ripen from September to December, the period that comprises the seed dispersal season (Fedriani and Delibes 2011).

In the Doñana region, seeds (0.6–0.8 g, 16.3×11.0 mm average size; Muñoz-Gallego et al. 2019) are dispersed by medium-sized carnivores, such as Eurasian badgers and red foxes (Fedriani and Delibes 2011). Both species are predominantly carnivorous but they usually consume fleshy fruits of multiple plant species during fall and winter (Fedriani and Delibes 2008). Thus, both species disperse *C. humilis* seeds throughout the dispersal season (October–December). Badgers usually defecate at latrines (i.e. feces aggregation up to 20 m; Garrote et al. 2022), where they partially or totally bury their feces with the local sandy substrate. Normally, several badgers share latrines for social communication by olfactory signals (Virgós 2017). Red foxes mark their territories defecating often at highly prominent sites (e.g. edge of unpaved roads; Suárez-Esteban et al. 2013) in a rather scattered spatial fashion (Fedriani and Wiegand 2014). *Chamaerops humilis* seed germination is hypogeal, with most seedlings emerging during the first spring-early summer. Although seedling mortality seems to be high during the first summer due to desiccation (approx. 70–80%), we found that ca. 50–60% of these apparently dead seedlings resprout after the fall rains (*unpublished data*).

The study was conducted at the Doñana National Park (37°9'N, 6°26'W; SW Spain) from October 2017 to December 2019. The climate is Mediterranean sub-humid and characterized by hot and dry summers, and most of the rain falls

during fall and winter (Żywiec et al. 2017). The Doñana area is a humanized and fragmented landscape, in which suitable habitat patches are isolated by cropland, towns, marshes or dunes. We set a 22-ha (800×300 m²) study plot (called Martinazo) in an area that has long experienced intensive human exploitation for decades. In particular, to create open areas of pasture for livestock ranching and cultivations, tree stands and scrubs were almost totally removed, and soil rotation was applied every 25 years during the early 20th century (Garrote et al. 2019). These intensive human activities finished when the area was declared a Biological Reserve in 1964. Although extensive livestock ranching still occurs in the area, other activities such as cultivation, timber exploitation and hunting are prohibited. Nowadays, the study plot is characterized by scattered *Quercus suber* and *Olea europaea* var. *sylvestris* trees within a dense Mediterranean scrubland (dominated by *Halimium halimifolium*, *Stauracanthus genistoides* and *Ulex* spp.) and wide pastureland with scattered shrubs limited to the east by marshland. Many vertebrate-dispersed woody plants (e.g. *Asparagus aphyllus*, *Pistacia lentiscus*, *Rubus ulmifolius*) are recolonizing the area after the cessation of human exploitation (Garrote et al. 2019, 2021). *Chamaerops humilis* density within our study plot was 8.3 individuals per ha (182 adults of which 57 and 63 were reproductive females and males, respectively).

Field sampling

During two consecutive seasons (October–December of 2017 and 2018), we conducted repeated transects (range = 0–4 per day) searching for fresh feces of badgers and foxes. This sampling method allowed us to track the temporal pattern of feces deposition (i.e. the timing of feces deposition). We intensely tried to distribute transects within the study plot evenly. To this end, we set 15 ‘starting points’ regularly distributed around the study plot perimeter. 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. Then, the observer came back following a different path leading to a departure point different from the starting one (Fedriani and Wiegand 2014). Each survey took about 1 hour and the average length was 1.9 ± 0.1 km. Altogether, we conducted 97 surveys (N = 65 and 32 in 2017 and 2018, respectively) covering 176 km (Fig. S2). During each transect, each recorded fresh feces was georeferenced using a submetric GPS Leica 1200 (Leyca Geosystems, Switzerland), tagged (sampling day, transect, as well as whether contained visible *C. humilis* seeds or not), and enclosed with wire mesh cages ($10 \times 10 \times 9$ cm³) (Fig. 1) to prevent trampling by ungulates.

From January 2018 to December 2019, we monitored seedling emergence and survival monthly in the enclosed

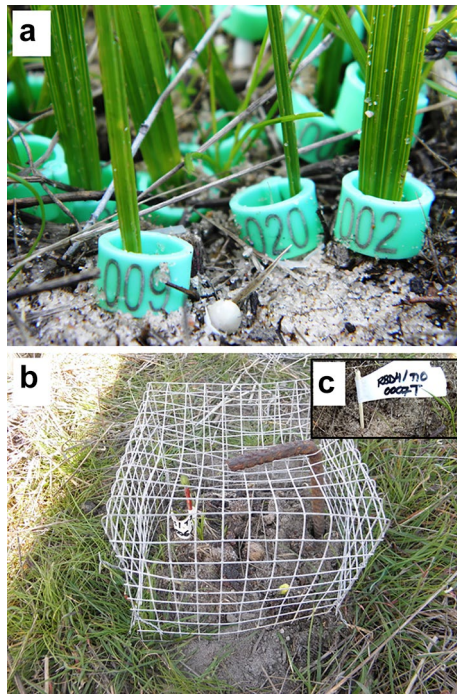


Fig. 1 Detail of exclusive colored numbered rings used for individual identification of *Chamaerops humilis* seedlings (a). Example of one excluded feces with a wire mesh cage (b) and the flag with its unique code (c)

carnivore feces. After two monitoring years, we recorded 312 seedlings from 25 feces (23 of badger and 2 of red fox). For the genotyping, we collected leaf material (3 cm in length) from 143 seedlings (i.e. 45.8%) when they had reached about 10 cm in height. We set three periods in which we collected leaf material: Period 1 in May 2018, Period 2 in December 2018, and Period 3 in May 2019 (Table 1). These periods were based on our previous experience monitoring of seedling emergence and survival. Specifically, Periods 1 and 3 were set before the substantial seedling death and desiccation in summer, and Period 2 was set after the autumn when many apparently dead seedlings can resprout. There were 169 seedlings that we could not genotype due to their small size ($\ll 10$ cm) preventing the material collection without compromising their survival or their death before the collection periods. Each genotyped seedling was marked with a unique colored numbered ring (Fig. 1). Importantly for our study, to confirm that leaf material removal did not affect seedling survival, we conducted a parallel field experiment outside the study plot from May to October of 2018. We caged 100 seedlings of similar size (ca. 10 cm) that had emerged within 12 badger feces. We clipped 50 seedlings (randomly selected), removing a similar amount of leaf material from each that was used for the genotyping (3 cm). The 50 remaining seedlings were left intact as the control treatment. The proportion of seedlings alive after

the first summer (i.e. the strongest mortality cause) did not differ between treatments (11 / 50 clipped vs. 13 / 50 control: $\chi^2 = 0.047$, $P = 0.83$).

Seedling genotyping

The DNA extraction and microsatellite genotyping is detailed in Jácome-Flores et al. (2019). Briefly, total genomic DNA was extracted following the manufacturer's protocol from approximately 25 mg of leaf material using the Isolate II plant DNA kit (Bioline, London, UK). All individuals were screened at 12 microsatellite markers and genotyped on an ABI PRISM 3130×1 DNA Sequencer (Applied Biosystems, Foster City, CA, USA). Alleles were scored manually using GeneMapper 3.7® (Applied Biosystems). Genotyping error rate of our set of microsatellite markers was calculated by running repeated, independent analyses for a total of 22 randomly chosen seedlings. Genotyping error (0.004%) was calculated as the ratio between the observed number of allelic differences and total number of allelic comparisons (Bonin et al. 2004) (Table S1). We also calculated the allelic dropout rates (0.055%) from 143 seedlings using MicroDrop (Wang and Rosenberg 2012) (Table S1).

Population genetics analyses

Genetic diversity and inbreeding

We obtained estimates of the genetic diversity of seedlings using the software INEST 2.2 (Chybicki and Burczyk 2009). INEST provides empirical Bayes estimates of observed and expected heterozygosity corrected for null alleles. INEST also provides unbiased multilocus estimates of inbreeding within a population, which are robust to the presence of null alleles. Specifically, INEST offers two approaches: PIM and IMM based on maximum likelihood and a Bayesian framework. We separately estimated the frequency of null alleles in our markers using both analytical approaches. Using the Bayesian approach (individual inbreeding model), INEST was run using *nfb* (null alleles, inbreeding coefficients and genotyping failures) and *nb* (null alleles and genotyping failures) models to detect the existence of inbreeding using 10^6 cycles, a thinning of 100 and a burning of 10^5 . The deviance information criterion was used to determine the best model.

Site (population) genetic structure

We estimated the pairwise kinship coefficient (F_{ij} ; Loiselle et al. 1995) among all pairs of seedlings and examined the FSGS using spatial autocorrelation analyses implemented in SPAGEDI 1.5 (Hardy and Vekemans 2015). Kinship coefficients can be sensitive to the presence of null alleles.

Table 1 Summary data of feces with genotyped *Chamaerops humilis* seedlings recorded during the field sampling conducted in the seed dispersal seasons of 2017 and 2018. It is shown the feces ID, the carnivore species, the geographic location, the date of feces deposition recorded as the day that we found the scat in the field sampling, the average ($\pm$ SE) linear distance to all recorded feces (the minimum and maximum linear distance to the nearest scat is shown in brackets),

the spatial isolation of feces classified as isolated (i.e. any feces around) and latrines (i.e. aggregated in latrines), the number of genotyped seedlings (the total number of emerged seedlings is shown in brackets), and the date of leaf material collection for the genotyping recorded as P1 (i.e. Period 1: May 2018), P2 (i.e. Period 2: December 2018), and P3 (i.e. Period 3: May 2019) (the number of genotyped seedlings in each period is shown in brackets)

Feces ID	Carnivore species	Geographic location	Deposition date	Average distance (m)	Spatial isolation	# Genotyped seedlings	Collection date
RBD1/T8/0041t	Eurasian Badger	37° 01' 23.71000" N; 6° 26' 17.86388" W	27-Sep-17	217.3 $\pm$ 177.5 (0.8–619.4)	Latrine	7 (19)	P1 (3); P3 (4)
RBD1/T8/0042t	Eurasian Badger	37° 01' 23.65956" N; 6° 26' 17.97697" W	27-Sep-17	216.2 $\pm$ 176.4 (0.6–617.0)	Latrine	2 (2)	P1 (1); P3 (1)
RBD1/T8/0038t	Eurasian Badger	37° 01' 22.78644" N; 6° 26' 26.00737" W	27-Sep-17	225.4 $\pm$ 122.4 (1.0–463.9)	Latrine	13 (24)	P1 (5); P2 (1); P3 (7)
RBD1/T8/0040t	Eurasian Badger	37° 01' 22.87221" N; 6° 26' 25.92797" W	27-Sep-17	223.6 $\pm$ 121.2 (0.8–459.9)	Latrine	4 (18)	P3
RBD2/FT/0001t	Eurasian Badger	37° 01' 24.97587" N; 6° 26' 15.56192" W	28-Sep-17	267.7 $\pm$ 179.2 (19.1–668.2)	Isolated	25 (30)	P1 (12); P2 (6); P3 (7)
RBD4/T10/0007t	Eurasian Badger	37° 01' 28.30201" N; 6° 26' 19.16591" W	2-Oct-17	248.8 $\pm$ 125.8 (2.5–529.8)	Latrine	19 (21)	P1
RBD4/T10/0005t	Eurasian Badger	37° 01' 28.91923" N; 6° 26' 19.32905" W	2-Oct-17	259.4 $\pm$ 124.7 (0.4–521.8)	Latrine	22 (45)	P1 (21); P3 (1)
RBD4/T10/0008t	Eurasian Badger	37° 01' 23.70402" N; 6° 26' 17.90543" W	2-Oct-17	216.7 $\pm$ 177.3 (0.6–618.3)	Latrine	3 (5)	P1 (1); P2 (1); P3 (1)
RBD6/T4/0007t	Eurasian Badger	37° 01' 22.77646" N; 6° 26' 26.10877" W	4-Oct-17	226.6 $\pm$ 122.7 (0.9–466.5)	Latrine	7 (9)	P1 (2); P3 (5)
RBD6/T3/0011t	Eurasian Badger	37° 01' 30.85070" N; 6° 26' 31.51297" W	4-Oct-17	385.7 $\pm$ 124.5 (90.6–578.8)	Isolated	4 (4)	P1
RBD6/T4/0008t	Eurasian Badger	37° 01' 22.89333" N; 6° 26' 25.92113" W	4-Oct-17	223.4 $\pm$ 120.8 (0.8–459.2)	Latrine	4 (14)	P1
RBD10/T10/0024t	Eurasian Badger	37° 01' 21.78184" N; 6° 26' 21.68696" W	9-Oct-17	234.0 $\pm$ 117.9 (34.8–554.9)	Isolated	6 (12)	P1 (5); P3 (1)

Table 1 (continued)

Feces ID	Carnivore species	Geographic location	Deposition date	Average distance (m)	Spatial isolation	# Genotyped seedlings	Collection date
RBD11/T11/0015z	Red Fox	37° 01' 28.24769" N; 6° 26' 19.12235" W	10-Oct-17	248.3 ± 126.3 (2.5–531.4)	Latrine	1 (1)	P1
RBD11/T11/0013t	Eurasian Badger	37° 01' 28.91103" N; 6° 26' 19.33621" W	10-Oct-17	259.2 ± 124.6 (0.1–521.6)	Latrine	3 (4)	P1
RBD11/T11/0014t	Eurasian Badger	37° 01' 28.90871" N; 6° 26' 19.33886" W	10-Oct-17	259.1 ± 124.6 (0.1–521.5)	Latrine	10 (37)	P1
RBD14/T3/0006t	Eurasian Badger	37° 01' 27.18458" N; 6° 26' 28.54507" W	13-Oct-17	269.6 ± 100.1 (45.4–450.0)	Isolated	4 (6)	P1 (3); P3 (1)

Therefore, we ran the analysis including only eight markers without evidence of null alleles (see Table 2). Tests for statistical significance of mean kinship coefficient values in each spatial distance class was conducted by (a) random shuffling (5000 times) individual geographical locations to define the upper and lower bounds of the 95% confidence interval around the null hypothesis that F_{ij} and pairwise spatial distances were uncorrelated, and (b) estimating 95% confidence intervals around mean F_{ij} values by bootstrapping loci (5000 times). Analyses were performed using 10 distance classes for which the number

of pairwise comparisons was approximately constant. By default, SPAGEDI creates the first distance class for the spatial groups of seedlings sharing spatial coordinates (i.e. seedlings within the same scat). Besides this first distance class encompassing seedlings with identical geographic coordinates, we set 10 additional distance classes maximizing the number of pairwise comparisons. We also computed the Sp statistic as $Sp = -b/(1-F_1)$, where b is the slope of the regression of F_{ij} on $\ln(\text{distance})$, and F_1 is the mean F_{ij} between individuals in the first distance class. The Sp statistic is a synthetic way of calculating the

Table 2 Genetic diversity for each microsatellite marker of *Chamae-rops humilis* seedlings. A , number of alleles per locus; AF , average of allelic frequencies; H_E and H_O , expected and observed heterozygosity accounting for null alleles; $null_{PIM}$ and $null_{IMM}$ are the estimates of null allele frequency given the PIM-based estimator (i.e. frequentist approach) and IMM-based estimator (i.e. Bayesian approach), respec-

tively; HWE, P -values for the presence of Hardy-Weinberg equilibrium after Bonferroni correction ($P=0.004$). For each estimate of genetic diversity, mean ($\pm$ SE) is provided. Minimum and maximum values are in brackets. Statistically significant values are indicated in bold

Locus	A	AF	H_E	H_O	$null_{PIM}$	$null_{IMM}$	HWE
CH26	15	0.066 (0.007–0.157)	0.896 (0.884–0.906)	0.876 (0.839–0.919)	0.027 (0.010–0.045)	0.014 (0.000–0.043)	0.000
CH13	3	0.261 (0.175–0.357)	0.728 (0.708–0.746)	0.707 (0.615–0.783)	0.231 (0.202–0.259)	0.218 (0.156–0.282)	0.000
CH19	4	0.244 (0.007–0.913)	0.162 (0.084–0.268)	0.140 (0.098–0.245)	0.023 (0.000–0.047)	0.023 (0.000–0.083)	0.334
CH14	6	0.108 (0.019–0.224)	0.772 (0.733–0.812)	0.750 (0.685–0.828)	0.330 (0.280–0.380)	0.353 (0.230–0.441)	0.000
CH7	3	0.323 (0.038–0.478)	0.561 (0.521–0.602)	0.563 (0.511–0.643)	0.004 (0.000–0.036)	0.030 (0.000–0.073)	0.008
CH21	2	0.405 (0.212–0.598)	0.558 (0.496–0.611)	0.530 (0.413–0.629)	0.204 (0.172–0.236)	0.190 (0.116–0.262)	0.000
CH15	10	0.099 (0.010–0.197)	0.850 (0.838–0.862)	0.868 (0.846–0.902)	0.005 (0.000–0.020)	0.014 (0.000–0.036)	0.000
CH6	5	0.197 (0.010–0.398)	0.726 (0.694–0.750)	0.767 (0.748–0.804)	0.000	0.013 (0.000–0.038)	0.072
CH3	9	0.098 (0.007–0.312)	0.821 (0.797–0.841)	0.818 (0.755–0.874)	0.120 (0.090–0.150)	0.120 (0.066–0.172)	0.000
CH25	5	0.198 (0.042–0.726)	0.451 (0.379–0.520)	0.440 (0.426–0.486)	0.000	0.008 (0.000–0.033)	0.012
CH5	3	0.327 (0.149–0.492)	0.618 (0.580–0.656)	0.664 (0.629–0.720)	0.000	0.020 (0.000–0.056)	0.270
CH17	5	0.197 (0.007–0.670)	0.497 (0.431–0.559)	0.466 (0.441–0.532)	0.003 (0.000–0.021)	0.014 (0.000–0.048)	0.359
Mean $\pm$ SE	5.8 $\pm$ 1.0	0.210 $\pm$ 0.029	0.637 $\pm$ 0.060	0.633 $\pm$ 0.062	0.079 $\pm$ 0.033	0.085 $\pm$ 0.032	0.088 $\pm$ 0.041

strength of the fine-scale spatial genetic structure (Veckman and Hardy 2004).

We also examined the overall site (i.e. population) genetic structure using the Bayesian Markov Chain Monte Carlo (MCMC) clustering in STRUCTURE 2.3.4 (Pritchard et al. 2000; Falush et al. 2003). We excluded four markers due to both the presence of linkage disequilibrium (CH7, CH15, and CH26) and strong evidence of null alleles (CH14) (see Table S2 and Table 2, respectively). We ran STRUCTURE assuming admixture and correlated allele frequencies (Pritchard et al. 2000). We conducted 20 independent runs for each value of $K=1-10$ to estimate the optimal number of clusters with 200,000 MCMC cycles, following a burn-in step of 100,000 iterations. We retained the 15 runs having the highest likelihood for each value of K . To define the most likely number of populations represented in our sample (optimal K), we examined the estimates of model log likelihood ($\log P(X|K)$, mean $\ln P(D)$ in the program output) for $K=1-10$. We also used the Evanno ΔK method (Evanno et al. 2005), implemented in STRUCTURE HARVESTER (Earl and vonHoldt 2012), to explore the number of populations best fitting the dataset. We used CLUMPP version 1.1.2 and the Greedy algorithm to align multiple STRUCTURE runs for the same K value (Jakobsson and Rosenberg 2007) and Distruct (Rosenberg 2004) to visualize the individual's probabilities of cluster membership.

Sibship reconstruction

We estimated sibling relationships among 143 seedlings using COLONY 2.0.6.4 (Jones and Wang 2010). We ran the model with 120 parent candidates (i.e. 63 males and 57 females; all adult reproductive palms present in the study plot, which were previously genotyped by Jácome-Flores et al. 2019). Conditions for the analysis include lack of known paternal and maternal sibships, polygamy, and inbreeding (as recommended by COLONY manual). We ran the model with eight markers since we had to exclude four markers due to both the presence of linkage disequilibrium (CH7, CH15, and CH26) and strong evidence of null alleles (CH14) (see Table S2 and Table 2, respectively). At the end of the computation, COLONY returns the best configuration with the maximum likelihood of parental identifications for each seedling. Then, we constructed a matrix to classify the dyads of seedlings as full-sibs (i.e. sharing both parents), half-sibs (i.e. sharing only one of two parents), or non-sibs (i.e. sharing no parents). The best configuration also informed about the presence of clones but in our case, this information was discarded given that all seedlings were independent genotypes. We estimated the proportion of these three sibship categories at three spatial scales: (i) within individual feces, distinguishing between isolated feces (i.e. ≥ 19.1 m from the nearest feces; Table 1) and

feces spatially aggregated at latrines (0.1–2.5 m from the nearest feces; Table 1), (ii) within latrines, and (iii) at the whole site.

Phenology and spatial isolation of the genetic rarity

We calculated the genetic rarity index to estimate the individual-level genetic rarity of seedlings (*sensu* Browne and Karubian 2016). First, we determined the corresponding relative frequency for each allele in each seedling. Then, we averaged across the relative frequencies of alleles within each locus with diploid genotype a, b to estimate the value of the genetic rarity index for seedling i :

$$\text{Genetic rarity index}_i = \frac{\sum_{l=1}^L (p_a + p_b)_l}{2L}$$

where L is the total number of loci, and p_a and p_b are the frequencies of alleles a and b at locus l . Note that p_a and p_b are equal in the case of homozygotes. Lower values of the genetic rarity index correspond to seedlings with genotypes containing rare, low frequency alleles.

We evaluated the effect of the timing of deposition and the spatial isolation of the feces on the genetic rarity of seedlings. We fitted a linear mixed model implemented in the R package *nlme* (Pinheiro et al. 2017). The timing of feces deposition (i.e. for each seedling, we counted the number of days since the first monitoring day until we detected the corresponding feces in the field), and the spatial isolation of seedlings (i.e. within isolated feces or within feces placed at latrines, see above) were included as the explanatory variables in the model. We also included feces as random effect to control for spatial heterogeneity. We checked the absence of collinearity between both explanatory variables ($r = -0.08$, $P = 0.37$) by using the R package *ppcor* (Kim 2015). We tested for significance based on Likelihood Ratio Test (LRT, hereafter) with χ^2 distribution implemented in the R package *lmtest* (Hothorn et al. 2015). We computed predicted marginal effects of the explanatory variables on the genetic rarity using the function *ggpredict* from the R package *ggeffects* (Lüdtke 2018).

Genetic rarity, spatiotemporal variation and seedling survival

To define the best predictors of seedling survival by the end of the monitoring (i.e. after 2 years), we fitted a set of competing Cox proportional-hazard regression models. The most parsimonious candidate models (i.e. $\Delta\text{AIC} < 2$) were selected by a stepwise method based on Akaike's Information Criterion (AIC; Burnham et al. 2011) using the function *stepAIC* from R package *MASS* (Ripley et al.

2013). In particular, we assessed whether seedling survival was affected by seedlings' genetic rarity, spatial isolation, timing of feces deposition, and timing of seedling emergence (i.e. covariates). We fitted these models using the *coxph* function from the R package *survival* (Therneau 2021). Our response variable, seedling survival was measured as the number of months between seedling emergence and death. Specifically, seedling survival was modeled as right-censored since surviving seedlings by the end of the monitoring could eventually die after the end of our study. We included feces identity as frailty (i.e. random) factor to control for potential spatial heterogeneity. The overall significance of Cox proportional-hazard regression models was tested by LRT. We also checked the potential collinearity among all covariates (Table S3) using the R package *ppcor* (Kim 2015). We only detected a moderate positive correlation between genetic rarity and spatial isolation ($r=0.24$, $P=0.02$; Table S3).

Results

Seed rain and genetic diversity of seedlings

We found a total of 99 feces (58 in 2017 and 41 in 2018) of which 68 were of badger and 21 of red fox. From these feces, 48 contained *C. humilis* seeds (36 in 2017 and 12 in 2018). After two years of monitoring, we detected a total of 312 emerged seedlings of which 309 were in 23 out of 41 badgers' feces and three in two out of seven red foxes' feces. Overall, we were able to genotype 143 seedlings (45.8%) located within 19 of 25 feces with emerged seedlings without compromising their survival (see Methods) (Table 1). From these seedlings, 104 were detected within feces located at latrines whereas 39 were found within isolated feces (Table 1). We only genotyped one seedling from a red fox scat which was located at a latrine. The average number ($\pm$ SE) of genotyped seedlings per feces was 7.53 ± 1.63 (range = 1–25). We genotyped on average $62.6 \pm 6.4\%$ (range = 13.3–100%) of emerged seedlings per feces (Table 1).

The overall F_{IS} after accounting for the presence of null alleles was 0.016 (0–0.035). We found that after accounting the presence of null alleles, the model without inbreeding outperformed (nb ; DIC 1 = 5062.794) the model with inbreeding (nb ; DIC 1 = 5065.468). Expected and observed heterozygosity corrected for the presence of null alleles were similar (Table 2). Expected heterozygosity ranged from 0.162 to 0.896 across our markers, with an average of 0.637 ± 0.060 (Table 2). The mean number of alleles per locus was 5.8 ± 1.0 (range = 2–15) (Table 2) (see also Table S4 for detailed genetic information per feces).

Site (population) genetic structure

Our results revealed positive FSGS at the first distance class, that is, inflated kinship among seedlings within the same feces, being 700-folds greater than expected under the null hypothesis of lack of genetic structure (Fig. 2; Table 3). The mean kinship within fecal samples was more than 32-folds times higher than that in the second distance class (i.e. 19.19 m on average between feces, that is, approximately within latrines; Fig. 2; Table 3). The overall strength of the FSGS estimated with the Sp statistic was 0.024.

Our STRUCTURE results supported the existence of three genetic groups according to Evanno K selection (Fig. S3). Interestingly, these three main genetic clusters were sub-structured in five sub-groups as suggested by the model log likelihood ($\ln P(D)$) (Fig. 3a). In particular, the individual probabilities of cluster membership were on average 0.319, 0.224, 0.192, 0.159, and 0.104 to the genetic clusters 1, 4, 5, 3, and 2, respectively (Fig. 3b). Feces showed on average a membership probability of 0.41 ± 0.05 , 0.20 ± 0.05 , 0.15 ± 0.05 , 0.12 ± 0.05 , and 0.12 ± 0.03 to the clusters 1, 3, 4, 5, and 2, respectively (Fig. 3c).

Sibship reconstruction

Sibling relationships among seedlings ($N=10,153$ pairs) varied within individual feces, within latrines and also at the whole site level (Fig. 4). Feces were classified as isolated ($N=4$ feces) and aggregated in latrines ($N=3, 4$, and

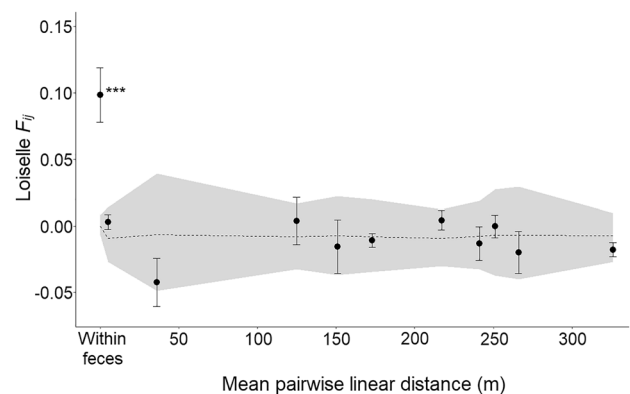


Fig. 2 Fine-scale spatial genetic structure of *Chamaerops humilis* seedlings with accounting for null alleles. Correlograms from spatial autocorrelation analysis using the Loiselle F_{ij} kinship coefficient and eleven distance classes being the first one those seedlings placed within feces (i.e. geographical groups). The number of pairwise comparisons is approximately constant for such distance classes. Black dots represent the mean kinship for each distance class. Grey area represents the 95% confidence intervals around the null hypothesis of lack of spatial genetic structure (i.e. the dashed line). Whiskers around average F_{ij} values in each distance class represent 95% confidence intervals generated by jackknifing loci. Observed kinship greater than expected is indicated with asterisks (***) $P < 0.001$

Table 3 Details of analysis of fine-scale spatial genetic structure for *Chamaerops humilis* seedlings. b_{log} is the slope estimate of the regression of the kinship coefficient (F_{ij}) on the natural logarithm of spatial distance jackknifed across loci, along with its standard error (SE). Sp estimates the overall strength of FSGS. Shown for each distance class are the: maximum distance, the number of pairwise

comparisons, the proportion of individuals represented at least once (% Participation), the coefficient of variation of the number of times each individual is represented (CV Participation), the mean distance among seedlings, the jackknifed mean kinship coefficient (F_{ij}), and the standard error of the kinship coefficient (F_{ij} SE)

				Distance class										
$b_{\log}$	$b_{\log}$ SE	Sp		1	2	3	4	5	6	7	8	9	10	11
−0.0022	0.0017	0.0024	Max distance	−1	19.19	69.96	145.16	153.16	200.36	234.43	247.16	252.93	269.43	434.02
			Number of pairs	923	1111	760	929	1194	646	914	908	1050	955	763
			% Participation	99.3	72.7	62.9	75.5	90.2	70.6	79.7	71.3	45.5	67.8	100
			CV Participation	0.65	0.9	0.99	1.01	0.77	1.3	1.1	1.16	1.11	1.06	2.08
			Mean distance	0	5.21	35.92	125.37	151.46	172.51	217.23	240.74	250.78	265.54	325.60
			F_{ij} Mean	0.098	0.003	−0.042	0.004	−0.016	−0.011	0.004	−0.013	0.000	−0.020	−0.018
			F_{ij} SE	0.020	0.006	0.018	0.018	0.020	0.005	0.007	0.013	0.009	0.016	0.005

7 feces, within 3 latrines) (Fig. 4a) (see also Table S4 for detailed genetic information per feces). The proportion of non-sibs was slightly greater within isolated feces than within feces at latrines (61.5% vs. 58%, respectively). Similarly, we found a greater proportion of half-sibs within isolated feces than within feces at latrines (32.9% vs. 26.4%; Fig. 4b). In contrast, seedlings within feces at latrines showed a greater average proportion of full-sibs (16% vs. 5.6%) than those within isolated feces (Fig. 4b). At larger spatial scales, latrines and site showed marked increases in the average proportion of non-sibs (87.3% and 91.2%, respectively) regarding the full- and half-sibs (Fig. 4b).

Phenology and spatial isolation of the genetic rarity

The genetic rarity index of seedlings ranged from 0.25 to 0.45, showing an average of 0.374 ± 0.003 (CV = 9.27%) (see also Table S4 for detailed genetic information per feces). The timing of feces deposition showed a significant effect on genetic rarity (LRT: $\chi^2 = 12.9$, $P < 0.001$; Table S5). The genetic rarity index slightly decreased as the seed dispersal season progressed, being 1.02-folds greater at the beginning than at the end (Fig. 5a). In other words, seedlings within feces deposited later during the seed dispersal season exhibited slightly rarer genotypes. The spatial isolation also had a significant effect on genetic rarity (LRT: $\chi^2 = 5.7$, $P < 0.05$; Table S5). Specifically, seedlings within isolated feces exhibited a slightly lower (0.97-fold) genetic rarity (i.e. slightly rarer genotypes) than those within feces at latrines (Fig. 5b).

Genetic rarity, spatiotemporal variation and demographic patterns

We monitored the survival of 105 of 143 genotyped seedlings for two years. We lost 38 seedlings during the monitoring

period due to ungulates trampling our wire mesh cages. On average, seedlings survived for 9.45 ± 0.47 months since emergence. Up to 81 of 105 seedlings (77.1%) died before the end of the monitoring (surviving on average 8.63 ± 0.53 months). The remaining 24 seedlings (22.9%) were alive by the end of the monitoring (surviving on average 12.17 ± 0.53 months).

The covariates of the best model (AIC = 598.6; Weighted AIC = 0.44) explaining seedling survival were genetic rarity, spatial isolation, timing of seedling emergence, and the second-order interactions between rarity and isolation as well as between emergence and isolation (Table S6). Additionally, there were two other models ($\Delta AIC < 2$) which could explain seedling survival showing predictive powers (i.e. Weighted AIC) of 0.21 and 0.16, respectively (Table S6). From these three models, only timing of seedling emergence ($\chi^2 < 10.42$, $P < 0.004$) and the interaction between emergence and isolation ($\chi^2 < 15.02$, $P < 0.0004$) showed significant effects on seedling survival (Table 4). Specifically, a later seedling emergence promoted a higher seedling survival. The significant effects of interaction suggested that a later emergence of seedlings within feces at latrines promoted a lower seedling survival regarding those within isolated feces. On the contrary, the remaining covariates included in the three selected models did not show any significant effect on seedling survival except for genetic rarity in the third model ($\Delta AIC = 2.01$; Weighted AIC = 0.16) in which it showed marginal significant effect as single covariate ($P = 0.08$) as well as the interaction between rarity and spatial isolation ($P = 0.09$) (Table 4).

Discussion

The assessment of spatiotemporal variation in the genetic makeup of recolonizing populations of pioneer species may significantly contribute to the conservation of ecological

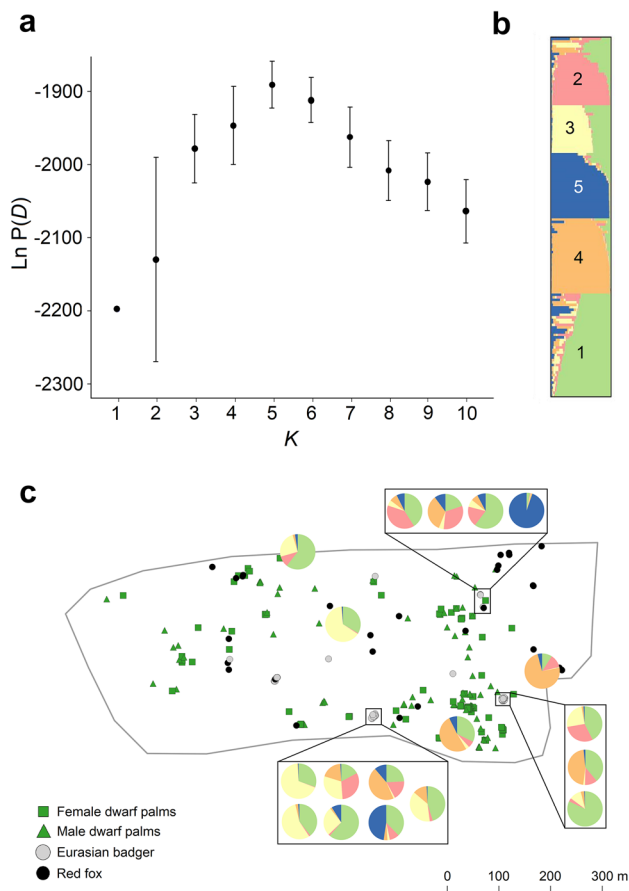


Fig. 3 Genetic structure of *Chamaerops humilis* seedlings with accounting for null alleles. Mean ($\pm$ SE) model log likelihood [Ln P(D)] over 15 runs of STRUCTURE for each K -value from 1 to 10 (a). STRUCTURE bar plots with seedlings sorted by the inferred number of $K=5$ genetic clusters. Each vertical bar represents a seedling and color segments are proportional to its membership in the four genetic clusters (b). Study plot (grey solid line) showing the seed rain generated by Eurasian badger (*Meles meles*; grey dots) and red fox (*Vulpes vulpes*; black dots) during seed dispersal seasons of 2017 and 2018. Female and male adult dwarf palms are represented by green squares and triangles, respectively. Pie charts represent feces with genotyped seedlings and the average probability of membership to the four genetic clusters. Feces within black squares were located at latrines (c)

processes underlying the recovery of human-altered regions. By combining genetic analyses and intensive field monitoring during two consecutive seed dispersal seasons, we revealed a significant spatiotemporal genetic structure in seedlings of a keystone plant species recolonizing Mediterranean human-altered areas (Garrote et al. 2021, 2022). In particular, we found that seedlings from single dispersal bouts (i.e. within the same fecal sample) had inflated kinship, but this positive FSGS diluted beyond their immediate neighborhood of plants. Furthermore, our results showed that the arrival of distinct genotypes was not constant throughout the seed dispersal season, with rare genotypes

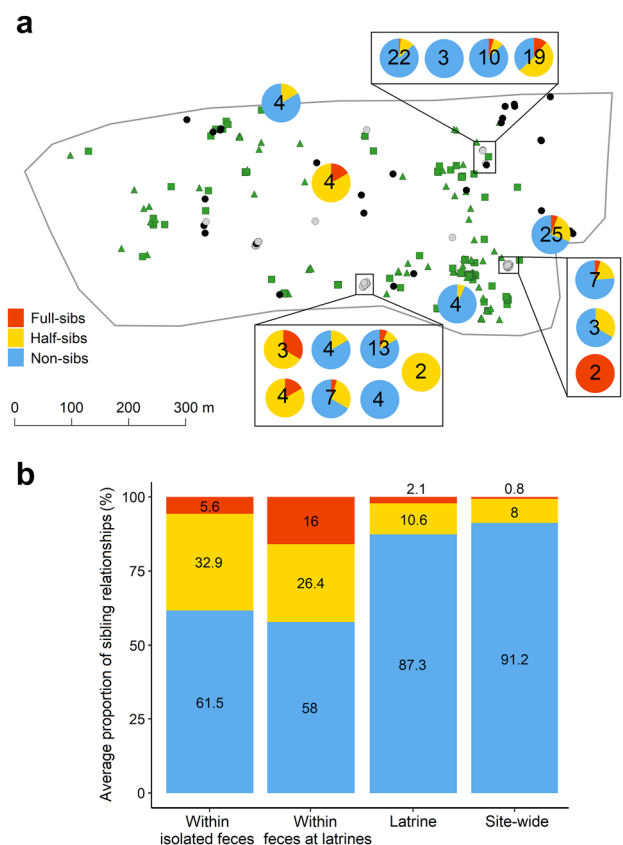


Fig. 4 Study plot (grey solid line) showing the seed rain during seed dispersal seasons of 2017 and 2018 generated by Eurasian badger (*Meles meles*; grey dots) and red fox (*Vulpes vulpes*; black dots). Female and male adult dwarf palms are represented by green squares and triangles, respectively. Pie charts represent feces with the number of genotyped seedlings and the proportion of their sibling relationships: full-sibs in orange, half-sibs in yellow and non-sibs in blue. Note the black squares focusing on feces placed at latrines (a). Average proportion of sibling relationships at three spatial levels: (i) within isolated feces vs. within feces placed at latrines, (ii) at latrines, and (iii) at the whole site (i.e. population) (b)

being more frequently deposited late in the season. Despite the observed spatial genetic structure, seedlings exhibited moderate to high genetic diversity levels and no evidence of inbreeding. Therefore, our results suggested substantial seed disperser-mediated *C. humilis* resilience to human-induced genetic impoverishment. However, additional biotic and abiotic factors may heavily influence plant recruitment and establishment beyond the genetic makeup of seedlings.

Lack of extensive spatial genetic structure in *Chamaerops humilis* seedlings

Our results revealed that seed dispersers inflated kinship in single dispersal events but facilitated genetic admixture beyond the immediate neighborhood through a recurrent spatial and temporal seed delivery. Badgers primarily drove

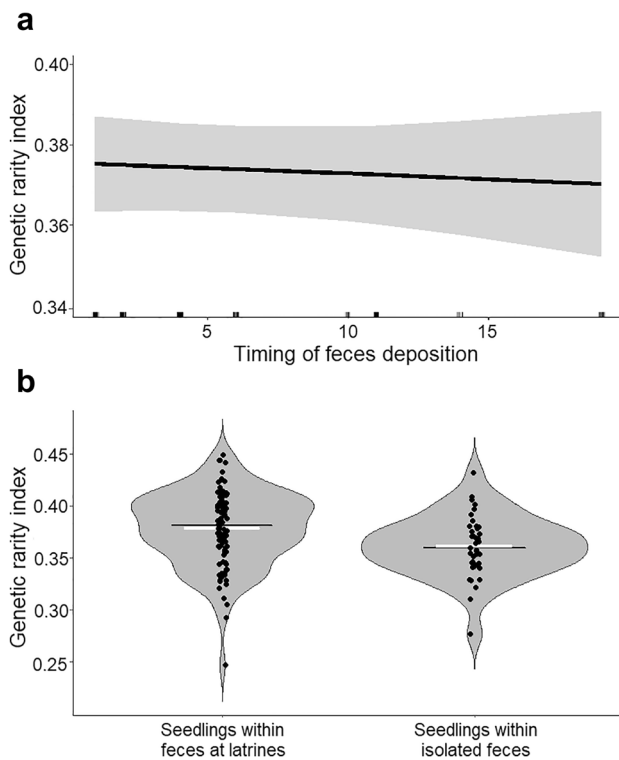


Fig. 5 Model-predicted mean effect of timing of feces deposition (i.e. the day from the beginning of the seed dispersal season in which the legitimate disperser delivered seeds) on the genetic rarity of *Chamaerops humilis* seedlings (**a**). Violin plot with the distribution of genetic rarity in terms of spatial isolation of seedlings (i.e. seedlings within isolated feces vs. seedlings within feces at latrines); black and white lines represent median and mean, respectively (**b**). Confidence intervals (95%) of prediction showed as grey area in (**a**). Note that lower values of the genetic rarity index correspond to seedlings with genotypes containing rare, low frequency alleles

this overall genetic pattern, since this species deposited the vast majority of seeds. In contrast, red foxes contributed to a minor fraction of seed rain. Our results align with previous work reporting a minor contribution of red foxes within the frugivore assemblage of *C. humilis* (Jácome-Flores et al. 2020; Garrote et al. 2022).

Even dispersers with the potential to cover long distances, such as primates, birds, or bats can exhibit spatially distinctive deposition patterns that result in the aggregation of genetically related seedlings (Bialozyt et al. 2014; González-Zamora et al. 2014; Ottewell et al. 2018; Sugiyama et al. 2018). We also found that seedlings from the same dispersal bout (with identical geographic coordinates) exhibited higher kinship than expected by chance. We posit that this inflated kinship among seedlings from the same dispersal event is driven by kin-structured dispersal (Torimaru et al. 2007), given the abundance of half-sibs detected at the feces level. In this regard, monitoring of seed disperser visitation rates has shown that dispersers often consume multiple fruits

daily from a reduced sample of maternal plants in the site (M. Selwyn, *personal communication*).

Interestingly, our results did not support positive fine-scale spatial genetic structure beyond the immediate neighborhood of seedlings belonging to a single dispersal event. Indeed, the proportion of genetically unrelated seedlings increased as we increase the spatial extent of our sampling. The lack of positive FSGS could be due to the admixture of diverse genotypes by recurrent defecation events of the highly mobile badgers over time and space. Usually, many badgers defecate repeatedly at several latrines within a region since they use them for social communication promoting thus, the arrival of numerous *C. humilis* seeds with diverse genotypes. This genetic pattern is similar to one found by Giombini et al. (2016) for seedlings of the tropical palm *Syagrus romanzoffiana* within tapir latrines in the southern limit of the Upper Paraná Atlantic Forest of South America. Indeed, these authors suggested that, even if spatially aggregated, the saplings recruited will probably show low genetic kinship due to the contribution of numerous feces over time (but see Karubian et al. 2015).

Independently of the explanatory mechanisms, our results suggest substantial resilience of *C. humilis* to face potential genetic bottlenecks during recolonization events. For instance, comparing our levels of genetic diversity in *C. humilis* seedlings with other palm species, we found moderate to high levels of genetic diversity in relation to seedlings of *Tahina spectabilis* ($H_E = 0.01\text{--}0.44$; Shapcott et al. 2020), *Copernicia prunifera* ($H_E = 0.41$; Vieira et al. 2016), and *Butia eriospatha* ($H_E = 0.49\text{--}0.53$; Nazareno and dos Reis 2014). However, our levels of genetic diversity were also similar to other palm species such as *Oenocarpus bataua* ($H_E = 0.67$; Diaz-Martin and Karubian 2021), or even much lower than *Euterpe edulis* seedlings ($H_E = 0.72\text{--}0.86$; da Silva Carvalho et al. 2015). Furthermore, the genetic build-up is apparent in the early stages of the natural recolonization (i.e. seedlings) as reflected by the similar genetic diversity in the reproductive adult plants (H_E of adults = 0.65 ± 0.05 ; unpublished data). This genetic diversity is higher than that found in other populations in the species distribution range (H_E of adults = $0.29\text{--}0.41$; Giovino et al. 2014).

The remarkable genetic diversity detected in seedlings can result, in part, from the seed dispersal ability of medium-sized dispersers and substantial genetic variation in the reproductive populations. Previous studies have found that medium-sized seed dispersers play an essential role in recolonizing human-altered areas by pioneer plant species (e.g., Peredo et al. 2013; Escribano-Ávila et al. 2014; Fedriani et al. 2018). Our study species is primarily dispersed by similar medium-sized carnivores (Fedriani and Delibes 2011), which often cover long distances in their daily movements (López-Martín 2017; Virgós 2017). Accordingly, previous studies in the study region found low genetic differentiation

Table 4 Results of Cox proportional-hazard models for seedling survival (i.e. months between seedling emergence and death) that were selected based on the Weighted AIC and with a $\Delta AIC < 2$ (see Table S6). *Rarity*: genetic rarity index; *Isolation*: spatial isolation; *Emergence*: number of months between seed dispersal and seedling emergence. Feces were included as random factor (i.e. frailty). Asterisks mark second-order interactions between covariates. Overall Likelihood-Ratio Test is shown for each model. Statistically significant covariates are in bold

Weighted AIC (ΔAIC)	Covariates	Coef ^a	exp(coef) ^b	SE (coef)	χ^2	P-value
0.44 (0)	Rarity	31.47	4.64e + 13	20.08	2.46	0.12
	Isolation	2.76	15.86	3.88	0.51	0.48
	Emergence	−0.61	0.54	0.21	8.45	0.004
	Rar * Iso	−15.97	1.16e-07	10.65	2.25	0.13
	Iso * Eme	0.39	1.47	0.11	12.58	0.0004
	Frailty(Feces)				0	0.93
	Overall LRT					< 0.0001
0.21 (1.46)	Rarity	32.73	1.64e + 14	19.96	2.69	0.10
	Isolation	3.03	20.70	3.86	0.62	0.43
	Emergence	−0.62	0.54	0.21	8.91	0.003
	Phenology	−0.02	0.98	0.02	0.52	0.47
	Rar * Iso	−16.86	4.76e-08	10.61	2.52	0.11
	Iso * Eme	0.39	1.48	0.11	13.15	0.0003
	Frailty(Feces)				0	0.93
	Overall LRT					< 0.0001
0.16 (2.01)	Rarity	34.28	7.75e + 14	19.41	3.12	0.08
	Isolation	2.69	14.71	3.77	0.51	0.48
	Emergence	−0.66	0.52	0.20	10.42	0.001
	Phenology	−0.13	0.88	0.10	1.73	0.19
	Rar * Iso	−17.44	2.67e-08	10.36	2.84	0.09
	Iso * Eme	0.41	1.51	0.11	15.02	0.0001
	Iso * Phe	0.06	1.07	0.05	1.42	0.23
	Frailty(Feces)				0	0.93
	Overall LRT					< 0.0001

^a The negative coefficient indicates that the factor has a positive effect on survival

^b Hazard ratio. The effect size of covariates

among populations of *C. humilis*, suggesting considerable gene flow in the study region (Jácome-Flores et al. 2018, 2019). Thus, carnivore seed dispersers seem to be playing a central role in the genetic admixture of recolonizing plant populations by promoting high levels of genetic diversity and low or nil inbreeding rates. Despite pollen dispersal in our system may be extensive, the contribution of pollinators *D. chamaeropsis* and *M. pallidulus* must be also considered because they likely contribute to mixing genotypes and thus, stimulating the gene flow in such human-impacted *C. humilis* populations (Anstett 1999; Dufaÿ and Anstett 2004; García et al. 2018).

Based on our findings, we emphasize the importance of conserving dispersal processes that promote high levels of genetic diversity and nominal inbreeding rates in recolonizing plant populations. These genetic attributes eventually provide resilience when facing rapid environmental changes, constituting the basis for future evolutionary processes and contributing to the maintenance of biological diversity (Lai-kre 2010; Hoban et al. 2013). However, human activities (e.g. habitat degradation, illegal hunting) may disrupt the seed dispersal process and thus cause a genetic impoverishment compromising the final fate of recolonizing plant

populations (Frankham et al. 2010; Markl et al. 2012; McConkey and O’Farrill 2016; Diaz-Martin and Karubian 2021). Therefore, we urgently recommend actions to conservationists and policy-makers that are pointed to ensure viable populations of seed dispersers and to facilitate the connectivity between source and recolonizing plant populations (e.g. carnivores; Draper et al. 2022).

Genetic rarity did not impact seedling survival

To our knowledge, we provided the first evidence of how common and rare genotypes recruit over time and space within plant populations. Specifically, our results revealed that rare genetic variants tended to arrive slightly later in the dispersal season and be more spatially isolated (i.e. lower conspecific density). We posit two alternative explanatory mechanisms for the reported late arrival of rare genetic variants. First, it could be related to the scarcity of fruits by the end of the season. This scarcity could force seed dispersers to visit other *C. humilis* populations to meet their energetic demands, increasing migration rates. A second non-exclusive mechanism would consist in asynchrony in fruiting phenology facilitating the late arrival of rare genotypes

in our recolonized site. For instance, if palms within our recolonized site reach a fruiting peak earlier, the migration from other *C. humilis* locations with a delayed phenology could explain the arrival of new genetic variants. The spatial isolation of rare genotypes may also result from those long-distance movements of seed dispersers among plant populations. Badgers moving long distances may deliver a certain proportion of feces with seeds isolated and far away from their habitual latrines (Fedriani et al. 2018). Importantly, we must carefully consider these findings due to the low strength of the size of effects. Therefore, there may be a considerable variation in genetic rarity explained neither by phenology of feces deposition nor by spatial isolation of feces.

Recently, it has been demonstrated that genetic rarity may have either positive or negative consequences on seedling survival and recruitment (Browne and Karubian 2016, 2018; Tito de Morais et al. 2020). While Browne and Karubian (2016, 2018) provided solid empirical evidences of rare genotypes advantage for seedling survival, Tito de Morais et al. (2020) found that less genetically related seedlings (i.e. rarer) had inflated mortality. These studies conducted sowing field experiments with seeds collected from mother plants (Browne and Karubian 2016), tracked the recruitment of naturally dispersed seeds collected in seed traps (Browne and Karubian 2018), or monitored the growth and survival of naturally established seedlings beneath mother plants (Tito de Morais et al. 2020). In contrast, we monitored the survival of naturally established seedlings dispersed by carnivores with only minor seed manipulation. In this regard, we propose combining sowing field experiments with monitoring natural recruitment as a powerful tool to evaluate how the genetic makeup of plants affects their recolonizing success.

In our study system, other ecological factors, such as spatial isolation and the timing of seedling emergence had a significant effect on seedling survival. Contrary to our expectations, genetic rarity was not a significant predictor by itself which indicates that, at least, its influence on seedling survival was smaller than those ecological variables. Overall, the late emergence of seedlings was associated with higher survival (but see Verdú and Traveset 2005). This pattern may be explained by delayed germination responding to neighbors within feces which can reduce intraspecific competition (e.g. Leverett et al. 2018). However, stressful abiotic conditions (e.g. drought and high temperatures) typical in Mediterranean habitats during late spring and summer may be harmful to seedlings emerging later. Therefore, this issue will require further attention in future investigations. Interestingly, seedlings can increase their survival benefiting from their spatial isolation since they can escape from negative frequency- and

density-dependent selection processes (Comita et al. 2014) that eventually occur in disproportionate seed clumps such as latrines (e.g. post-dispersal seed predation; Srbek-Araujo et al. 2017; Authors *personal observations*). Taken together, our results highlight the importance of intensive monitoring of seed rain throughout the dispersal season to record in detail how the genetic makeup is temporarily and spatially shaped in plant populations.

Concluding remarks

By exploring the spatiotemporal variation of genetic diversity and genetic rarity of pioneer plant populations, we shed light into the mechanisms underlying the natural recolonization of Mediterranean human-altered areas and their effects on recruitment and seedling fate. The study of plant-animal interactions from a genetic perspective provides crucial information for plant conservation and the recovery of genetic plant resilience. Certainly, some animal dispersal vectors strongly assist pioneer plants in lessening potential genetic bottlenecks during recolonization events of human-altered habitats. Therefore, the conservation of dispersal vectors and the connectivity between plant populations seem indispensable for the improvement of genetic plant resilience (García-Dorado and Caballero 2021; DeWoody et al. 2021; but see Teixeira and Huber 2021) and the expansion of plant ranges facing the alarming future predictions of global warming (IPCC 2018; González-Varo et al. 2021).

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Data availability Data deposited in Figshare repository (<https://doi.org/10.6084/m9.figshare.21723884.v1>).

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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