



Non-native Mammals Are the Main Seed Dispersers of the Ancient Mediterranean Palm *Chamaerops humilis* L. in the Balearic Islands: Rescuers of a Lost Seed Dispersal Service?

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Megafauna extinctions often lead to the disruption of plant-animal interactions, such as the seed-disperser mutualisms, which might entail severe consequences for plant populations and entire communities. Interestingly, the contemporary persistence of anachronistic plant species might be possible thanks to surrogate dispersers or seed dispersal "rescuers". We know very little on how these relevant functional replacements are contributing to the performance of present-day plant-frugivore networks. The dwarf palm *Chamaerops humilis* L. is a Mediterranean endemism with fleshy fruits and typically dispersed by mammals. Despite its ecological importance and wide distribution in some of the Mediterranean islands, no information exists about its seed dispersal on these depauperated-fauna systems. In this study, we aim at identifying and quantifying the relative importance of introduced frugivores on the island of Mallorca (Balearic Islands), where no native terrestrial mammals exist. Specifically, we assess for the first time the seed dispersal effectiveness (SDE) for *C. humilis* on islands; we evaluate the quantitative component by fecal and regurgitation sampling surveys, and the qualitative component by means of seed germination experiments and seedling growth measures. Introduced goats (*Capra hircus* L.) and pine martens (*Martes martes* L.) were the local mammal fruit consumers of *C. humilis* identified in our study sites. Results suggest that goats are much more important quantitatively than pine martens, due to the high number of fruits handled in each foraging bout and their extremely high abundance on the island. However, pine marten-ingested seeds showed the highest final seedling emergence success and seedling growth, thus its qualitative contribution on *C. humilis* seed dispersal is higher than that of goats. Overall, SDE was almost 9-fold higher for goats than for pine

martens. We conclude that these two non-native mammal species are effective seed dispersers of *C. humilis* in this and probably other Mediterranean islands, where humans led to the extinction of its native seed dispersers, as it was probably the case of the goat-like *Myotragus balearicus* in the Balearic Islands.

Keywords: anachronism, goat, megafauna extinction, *Myotragus balearicus*, pine marten, seed dispersal effectiveness, seedling emergence, seedling growth

INTRODUCTION

Numerous extinctions of large terrestrial vertebrates driven by human activity have taken place during the Late Pleistocene and Early Holocene (Ceballos et al., 2015; Faurby and Svenning, 2015). This has occurred in most continents, and well-studied cases are the extinctions of megafauna species in the American continent, such as saber-toothed cats (*Smilodon* spp.), mammoths (*Mammuthus* spp.), and giant ground sloths (*Megalonyx jeffersonii*) (Janzen and Martin, 1982; Sodhi et al., 2012). On islands worldwide, the rate of extinction of terrestrial mammals after the arrival of humans was c. 30%, being fateful for the orders Proboscidea, Xenarthra and Bymalagasia and quite strong for Artiodactyla, Carnivora, and the rodent infraorder Hystricognathi (Alcover et al., 1998). These events not only led to the vanishing of many populations and species, but also to the disruption and reshaping of ecological interactions which likely altered the structure and function of entire communities and ecosystems. In fact, severe impacts of large vertebrate extinctions on the ecosystem physical and trophic structure, plant community composition, and diversity, ecosystem biogeochemistry, and regional and global climate have been described (Dirzo et al., 2014; Bello et al., 2015; Ripple et al., 2015; Malhi et al., 2016; Smith et al., 2016). In addition, the loss of megafauna can affect ecological interactions in three ways: leading to co-extinctions, adaptative shifting, and evolutionary anachronisms (Galetti et al., 2018). This last concept, described for the first time several decades ago by Janzen and Martin (1982), is defined in a context of frugivory as “extant interactions between animal frugivores and plants involving traits that show striking unfit patterns to an extant fauna” (Guimarães et al., 2008, p. 2). Typical examples are fruits with huge seeds which are dispersed inefficiently by the contemporary frugivore assemblages, like avocado (*Persea americana*) (Cook, 1982), osage orange (*Maclura pomifera*) (Janzen and Martin, 1982), or Florida torreya (*Torreya taxifolia*) (Barlow, 2001). Anachronisms can also show up through antagonisms, such as the presence of spines or other plant defenses against large herbivores that no longer exist (e.g., Bond et al., 2004). These unfit patterns could be explained if we consider all the extinct megafauna which would have acted as legitimate dispersers or herbivores in the past, exerting selective pressures on plant traits (Barlow, 2000; Guimarães et al., 2008).

Seed dispersal is a key ecological process in the life cycle of plants because it allows propagules to move away from the maternal environment, providing a higher propagule survival probability, maintaining the genetic flow, and enabling the

colonization of vacant habitats (Levey et al., 2002; Medel et al., 2009; Schupp et al., 2010). Therefore, the disruption of this relevant ecological service due to the extinction of effective seed dispersers can result in serious consequences for plant populations: modification of range and spatial distribution (e.g., Meehan et al., 2002; Rotllàn-Puig and Traveset, 2016), decrease in the total number of seed successfully dispersed, germinated and established (e.g., Galetti et al., 2006; Wotton and Kelly, 2011; Traveset et al., 2012), alteration of the seed shadow (e.g., Beaune et al., 2013; Bueno et al., 2013), restriction of the gene flow and genetic structure increase (e.g., Collevatti et al., 2003; Caughlin et al., 2015), interruption of long-distance dispersal (e.g., Pérez-Méndez et al., 2016; Pires et al., 2018), and shift of phenotypic selection on seed size (e.g., Galetti et al., 2013). This often ends in a collapse in the life cycle and species decline (Valiente-Banuet et al., 2015; Rumeu et al., 2017; Galetti et al., 2018). On islands, where communities are depauperate and plants may be very specialized in their dispersers (González-Castro et al., 2012), the negative outcomes from such disruptions are even greater (Traveset and Richardson, 2014). The disappearance of frugivorous forest birds (e.g., moas, piopio *Turnagra capensis*, huia *Heterolocha acutirostris*) as important dispersers of many woody plants on New Zealand (Clout and Hay, 1989; Wood et al., 2008), or the reduction of flying foxes on tropical Pacific islands (McConkey and Drake, 2006) are some examples of disrupted dispersal service on islands, although the list is long and increases (e.g., Rogers et al., 2017; Rumeu et al., 2017). In the Mediterranean basin, few studies have been carried out on the disruption of plant-disperser mutualisms (e.g., Traveset, 2002; Traveset et al., 2012). Interestingly, the persistence of large-fleshy-fruited species has often been possible thanks to extant small-sized frugivores mammals such as rodents (Jansen et al., 2012), and also to introduced carnivores or livestock (Janzen and Martin, 1982), which may act as “surrogate Pleistocene dispersal agents” (*sensu* Janzen, 1982). Other examples have been documented from other systems. For instance, in the Balearic Islands, introduced pine martens (*Martes martes*) replace, at least partially, the native lizards which presumably used to be the only legitimate dispersers of the native shrub *Cneorum tricoccon* until recently (Traveset, 1995; Celedón-Neghme et al., 2013). Therefore, contemporary frugivore assemblages, even though in a suboptimal way (Guimarães et al., 2008), can act as “rescuers” of the seed dispersal service of anachronistic species, mitigating the effects of previous animal extinctions, and avoiding the vanishing of ecological interactions (Zamora, 2000; Valiente-Banuet et al., 2015; Rumeu et al., 2017; Cares et al., 2018).

On Mallorca island (Balearic archipelago), the native vertebrate fauna of the Upper Pleistocene and the Holocene was composed only of three endemic species: the cave goat *Myotragus balearicus* (Artiodactyla: Bovidae; 25.19–33.34 kg, Palombo et al., 2008), the giant dormouse *Hypnomys morpheus* (Rodentia: Gliridae; 0.23 kg, Moncunill-Solé et al., 2014) and the Balearic shrew *Nesiotites hidalgo* (Soricomorpha: Soricidae; 0.023–0.031 kg, Bover et al., 2008; Moncunill-Solé et al., 2016). The cave goat was thus the only medium-sized herbivorous mammal present on the islands (specifically, on Mallorca, Menorca and Cabrera). Its extinction took place during the Holocene, around 3000–2000 BC, and has been associated to the first arrival of humans to these islands (Bover and Alcover, 2008; Bover et al., 2016). Nowadays, the only non-flying mammals present in the Balearics have all been introduced by man, including goats, sheep, cows, pigs, dogs, as well as rodents (Bover and Alcover, 2008; Valenzuela and Alcover, 2013a). The wild carnivore the weasel (*Mustela nivalis*) appears to have been imported by Talaiotic people (prior to 123 BC) (Valenzuela and Alcover, 2013b). Subsequently, during the Roman period (123 BC–534 AD), the domestic cat (*Felis catus*) and the pine marten (*M. martes*) were introduced (Valenzuela and Alcover, 2015), and the common genet (*Genetta genetta*) was also probably introduced previously to the Muslims arrival (656–773 AD; Delibes et al., 2017b). The raccoon (*Procyon lotor*) and the coati (*Nasua nasua*) have been established very recently (in 2006 and 2004, respectively) on the island (Mayol et al., 2009; Pinya et al., 2009). However, very little is known about the ecological role of these introduced vertebrate species on the dynamics and composition of island communities.

In the present study, we aim at identifying and quantifying the relative importance of introduced seed dispersers for the dwarf palm *Chamaerops humilis* L. on Mallorca. This endemic palm is known to be mammal-dispersed elsewhere (Fedriani and Delibes, 2011) and we thus expect that non-native mammals play the role of dispersers in this island. In the few areas of continental Europe where its seed dispersal has been studied (Table 1), carnivorous mammals such as the European badger (*Meles meles*) and the red fox (*Vulpes vulpes*) have been described as its legitimate dispersers, and rabbits (*Oryctolagus cuniculus*) and some ungulates, like the wild boar (*Sus scrofa*), deer (Cervidae) and the domestic goat (*C. hircus*), act as occasional and suboptimal dispersal agents (Fedriani and Delibes, 2008, 2011; Delibes et al., 2017a). On islands, for which information is less available, only a few species have been described as consumers of the palm fruits (see Table 1). In Mallorca, its seeds have only been documented from *G. genetta feces* (Alcover, 1984; Clevenger, 1995), and no study has been carried out on the seed dispersal of this plant despite its high ecological, cultural and economic value (Guzmán et al., 2017).

The specific questions addressed in this study are the following: (1) Who are currently the main vertebrate fruit consumers of *C. humilis* on Mallorca? (2) How quantitatively and qualitatively effective are such fruit consumers as seed dispersers? To estimate the quantitative component of the seed dispersal effectiveness (SDE) of potential seed dispersers, we searched for mammal droppings and regurgitations, throughout linear

transects in areas where this plant is abundant. On the other hand, the qualitative component of SDE for each seed disperser was assessed by means of a seed germination experiment using *C. humilis* seeds extracted from mammal samples as well as control (i.e., non-ingested) seeds. From our results, we discuss on the functional role of non-native mammal species as seed dispersers of this ancient Mediterranean palm on islands.

MATERIALS AND METHODS

Study Area

The study was carried out in the Northeast of the Mallorca island, specifically in the North of Serra de Tramuntana (municipality of Pollença) and in the North of Serra de Llevant (municipality of Artá). Four study sites, called “Cala Bóquer”, “Cap de Formentor”, “Ermita de Betlem” and “Es Caló” (Figure 1), were chosen. The predominant forest species are Aleppo pine (*Pinus halepensis*) and oak (*Quercus ilex*). Several shrub species, such as *C. humilis*, *Olea europaea* var. *sylvestris*, *Pistacia lentiscus*, *Erica multiflora*, *Cistus monspeliensis*, *Ampelodesmus mauritanicus*, and *Calicotome spinosa* are abundant over this territory. The climate of the Balearic archipelago is typically Mediterranean, characterized by two rainy seasons, a hot dry summer and a soft winter. Monthly rainfall on Mallorca varied between 0 and 107.2 mm during 2017, with the most rain falling in January and September, and extreme drought in May. Annual average temperature was 18.2°C (data from *Red de Estaciones Meteorológicas de Baleares*¹).

Study Species

The endemic Mediterranean dwarf palm *Chamaerops humilis* L. (Arecaceae) is a representative species of the Pre-Pliocene paleotropical ancestral lineages (Thompson, 2005). It is very likely that this ancient palm was in the Balearic Islands long before the arrival of the first settlers since its presence in the eastern coast of the Iberian Peninsula (Arroyo et al., 2004; Pérez-Obiol et al., 2010) and in other Mediterranean islands (Sardinia; Biondi and Filigheddu, 1990) is very old, previous to the Mediterranean Sea desiccation. Nevertheless, this remains uncertain so far due to the lack of any pre-anthropogenic evidence in both pollen and fossil records (Carrión, 2012), which is not surprising because of the poor preservation of this species and the little amount of pollen that scatters (F. Burjachs, pers. comm.) due to, probably, its insect-pollinated syndrome (Carrión, 2002). In Mallorca, this dioecious palm is relatively abundant currently, especially in Serra de Tramuntana and in the North of Serra de Llevant (García and Morey, 1989; Bioatles—Govern de les Illes Balears²). It flowers during spring (March–May) and the fruits ripen in autumn (September–November). Its fleshy fruits are poly-drupes (Herrera, 1989). Unripe fruits are bright green, turning to dull yellow to brown when ripe. The seed (usually 0.6–0.8 g, 16.3 × 11.0 mm average dimensions, Delibes et al., 2017a) comprises a small cylindrical embryo (2 mg), which is surrounded by several layers, from inner to outer: (1) a nutritious endosperm, (2) a

¹<http://balearsmeteo.com/>

²<http://bioatles.caib.es/serproesfront/VisorServlet>

TABLE 1 | Mammal species that consume *C. humilis* fruits described in the Mediterranean basin so far, indicating the system (island or mainland), the region, whether they are native or not, the frequency of occurrence of dwarf palm fruits in their diet, and the reference of the study.

System	Mammal consumer	Native or non-native	Region	Frequency of occurrence	References
Island	Common genet (<i>Genetta genetta</i>)	Non-native	Balearic Islands (Spain)	8.0 ^a	Clevenger, 1995
	Sardinian fox (<i>Vulpes vulpes</i> subsp. <i>ichnusae</i>)	Non-native	Sardinia (Italy)	<4.0 ^a	Farris et al., 2017
	Sardinian wild boar (<i>Sus scrofa meridionalis</i>)	Non-native	Sardinia (Italy)	3.0 ^b	Pinna et al., 2007
Mainland	European badger (<i>Meles meles</i>)	Native	Almería (Spain)	~30.0 ^a	Requena-Mullor et al., 2016
			Huelva (Spain)	<20.0 ^c	Revilla and Palomares, 2002
				Presence	Fedriani and Delibes, 2008
				Presence	Fedriani and Delibes, 2011
				Presence	Perea et al., 2013
	Red fox (<i>Vulpes vulpes</i>)	Native	Almería and Murcia (Spain)	2.77 ± 1.69 ^a	Cancio et al., 2017
			Barcelona (Spain)	35.05 ^a	Martín, 2008
			Huelva (Spain)	8.0 ^d	Fedriani, 1996
				Presence	Fedriani and Delibes, 2008
				5.0 ^e	Perea et al., 2013
				Presence	García-Cervigón et al., 2018
				Presence	V. M. Zapata, pers. comm.
				Presence	J.M. Fedriani, pers. obs.
				Presence	Fedriani and Delibes, 2008
				Presence	García-Cervigón et al., 2018
	Wild boar (<i>Sus scrofa</i>)	Native	Huelva (Spain)	2.0 ^e	Perea et al., 2013
				Presence	García-Cervigón et al., 2018
	Barbary macaque (<i>Macaca sylvanus</i>)	Native	Cascades d'Ouzoud (Morocco)	Presence	El Alami and Chait, 2017
			Gibraltar (United Kingdom)	Presence	Schurr et al., 2012
	African golden wolf (<i>Canis anthus</i>)	Non-native	Tlemcen (Algeria)	34.96 ^a	Eddine et al., 2017
Egyptian mongoose (<i>Herpestes ichneumon</i>)	Non-native	Huelva (Spain)	1.0 ^d	Palomares and Delibes, 1991	
Domestic goat (<i>Capra hircus</i>)	Native	Sevilla (Spain)	Presence*	Delibes et al., 2017a	
Red deer (<i>Cervus elaphus</i>)	Native	Albacete (Spain)	Presence*	Castañeda et al., 2018	

*Experimental study.

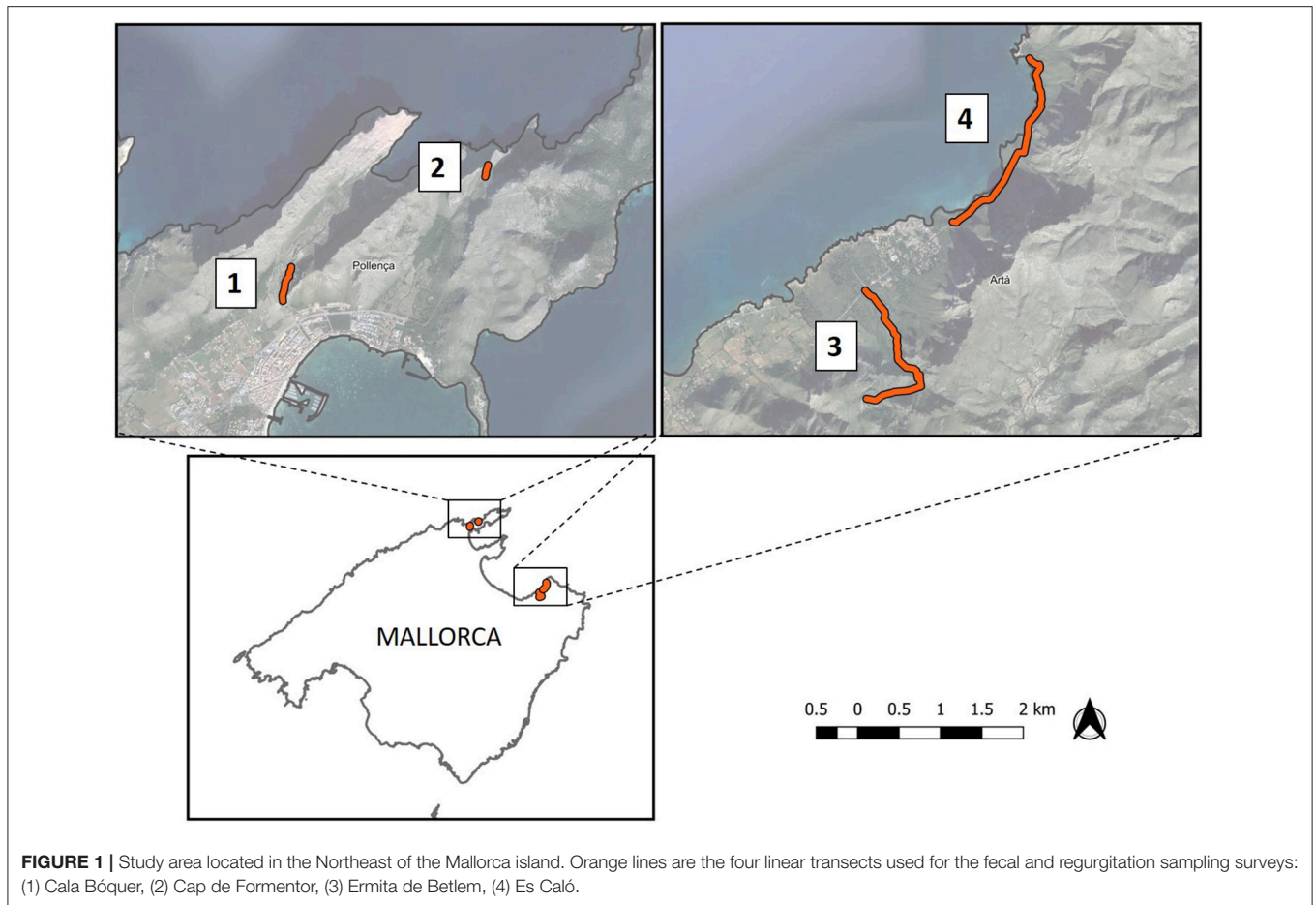
^aPercent in feces.^bPercent in stomach.^cPercent estimated biomass ingested.^dMinimum number of seeds in feces.^eNumber of seeds per feces (log scale).

wide woody layer or endocarp, (3) a fleshy and fibrous mesocarp (the pulp, that smells strongly of rancid butter when ripe), and (4) the thin outer layer or exocarp (González-Benito et al., 2006; Hasnaoui et al., 2009). The medium-sized seed is usually large enough to preclude their consumption by birds, so this plant species belongs to the known “mammal-dispersal syndrome”. Occasionally, though, birds may remove some fruits and thus transport seeds to different distances; specifically, one songbird (*Turdus merula*) was once observed picking one fruit and leaving with it in its bill (R. Muñoz-Gallego, pers. obs.). The dwarf palm seeds are commonly predated by beetles. At least, two non-native scolytine species have been described to bore into *C. humilis* seeds in the continent, *Coccotrypes dactyliperda* and *Dactylotrypes longicollis*, taking place as both pre- and post-dispersal events. Thus, these beetles bore the pulp and endocarp of fruits still

attached to the mother plant, dropped from inflorescences, and also of dispersed (and depulped) seeds (Rodríguez et al., 2014; this study). Fruits are attached to infructescences (or ramets) of up to 30 cm long (20–40 fruits per ramet, Fedriani and Delibes, 2011) and located at 10–30 cm from the ground level. Germination is hypogeal and remote, with most seedlings emerging during spring time. Moreover, it has a well-known ability to thrive on poor nutrient soils (Herrera, 1989).

Seed Dispersal Effectiveness: Quantitative and Qualitative Components

Seed dispersal effectiveness (SDE) is defined as the “number of new adult plants produced by the dispersal activities of a disperser” (Schupp, 1993, p. 16). SDE can be quantified as the number of seeds dispersed by a dispersal agent (quantitative



effectiveness) multiplied by the probability that a dispersed seed produces a new adult (qualitative effectiveness): $SDE = \text{Quantity} \cdot \text{Quality}$. In our study, the quantitative component of SDE was obtained by recording the number of mammal samples that contained *C. humilis* seeds multiplied by the mean number of seeds per sample (Figure 2). This metric was then corrected by the distance (km) of each transect (e.g., Suárez-Esteban et al., 2013). On the other hand, the qualitative component (i.e., quality of treatment in the mouth and gut) was assessed by recording seedling emergence and seedling growth. The latter was determined by measuring both seedling length and dry weight (Figure 2). Finally, the SDE landscape (sensu Schupp et al., 2010), a visual representation of effectiveness and the relative contribution of each disperser, was estimated by multiplying the quantity component (number of dispersed seeds per distance sampled) by the quality component (emergence success). The landscape was plotted with the code provided by Jordano (2014) with Rstudio v.1.1.383 (R Core Team, 2017).

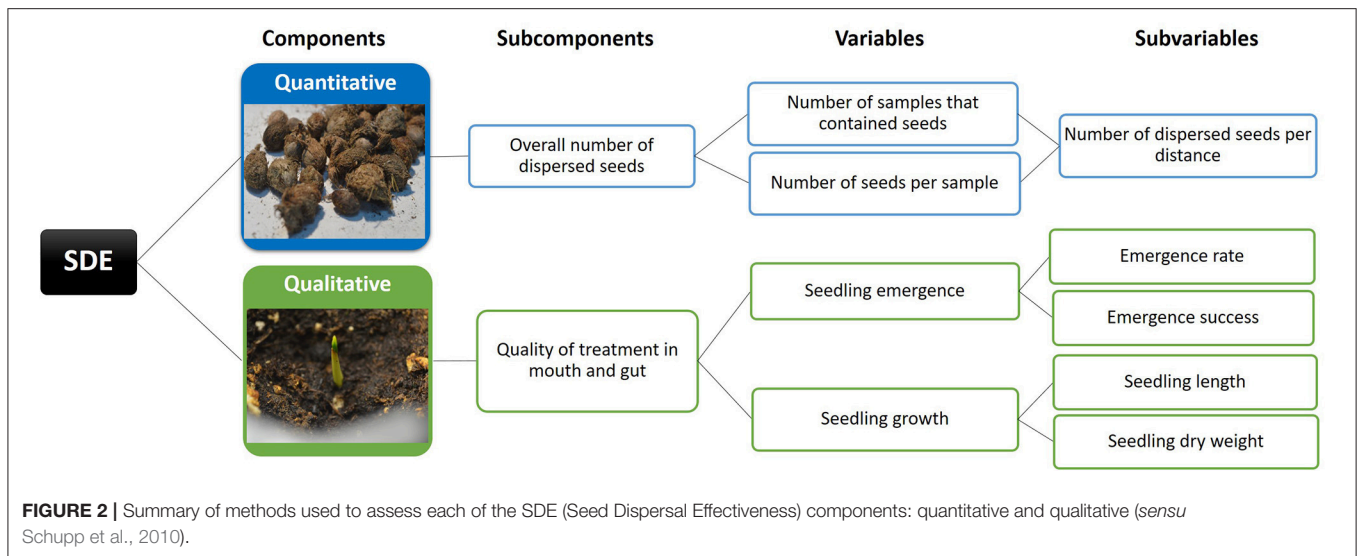
Fecal and Regurgitation Sampling Surveys

In November of 2017, we searched for fresh mammal droppings and regurgitations belonging to the second half of the 2017 fruiting season (determined by their non-dry appearance), along forest tracks and adjacent forest and garrigues. The four transects

surveyed are shown in Figure 1: “Cala Bóquer” with 0.44 km in length (start point: $39^{\circ} 54' 53.55''$ N, $3^{\circ} 4' 55.60''$ E), “Cap de Formentor” with 0.15 km (start point: $39^{\circ} 55' 46.54''$ N, $3^{\circ} 6' 39.93''$ E), “Ermita de Betlem” with 2.25 km (start point: $39^{\circ} 44' 56.80''$ N, $3^{\circ} 18' 41.23''$ E), and “Es Caló” with 2.6 km (start point: $39^{\circ} 45' 23.60''$ N, $3^{\circ} 19' 25.80''$ E). The first two are located in Serra de Tramuntana and the last two in Serra de Llevant. Mammal feces were identified by their color, shape, smell and associated footprints (Bang and Dahlstrom, 2001). Fecal and regurgitated samples were air dried at room temperature and stored individually in paper bags. Each fecal sample was later washed using a sieve under running water, and seeds were immediately and carefully removed and dried (Fedriani and Delibes, 2009).

Seed Germination Experiment

We sowed *C. humilis* mammal-ingested seeds as well as control seeds (i.e., non-ingested). To obtain control seeds, ripe fruits were collected during the sampling surveys from individuals distributed along the transects. Fruit ingestion and digestion have two effects on seeds that usually enhance their germination: (1) neutralization of the pulp inhibitory effect due to the removal of the pulp, and (2) seed coat scarification effect (Samuels and Levey, 2005). To separate both effects, we used two types of



control seeds: intact fruits and fruits with the pulp manually removed. Therefore, we established five seed treatments for the germination experiment: (1) control 1 or “control seeds with pulp” ($n = 43$), (2) control 2 or “manually-depulped control seeds” ($n = 44$), (3) seeds regurgitated by goats ($n = 99$), (4) seeds spit out by goats ($n = 80$), and (5) pine marten-ingested seeds ($n = 24$). Distinction between seeds spit out and seeds regurgitated was required as the former experience a mechanical and chemical treatment only in the mouth while the latter spend also a given amount of time within the stomach in contact with the gastric juices. So, we categorized spit and regurgitated seeds based on our previous field observations and our work on other similar systems (Delibes et al., 2017a; Castañeda et al., 2018). Regurgitated seeds showed little persisting pulp, a wear out aspect, and often an irregular surface. Spit seeds have generally attached most of the pulp and a much less wear out aspect. Firstly, collected seeds were examined visually with 20–40 x magnification glasses, and traits which could affect germination, such as seed predation by insects, were recorded. Seed predation was estimated from the presence and number of holes on the endocarp (Rodríguez et al., 2014). In January 2018, both control ($n = 87$) and mammal-ingested seeds ($n = 203$) were sown individually in pots within 18 pot-trays (18 × 8 × 8 cm) with commercial substrate. Sown seeds ($n = 290$) were incubated in a chamber under controlled environment ($25 \pm 5^\circ\text{C}$, $50 \pm 5\%$ relative humidity, 12-h dark/12-h light photoperiod, uninterrupted ventilation, watering periodically; Salvador and Lloret, 1995; González-Benito et al., 2006; Hasnaoui et al., 2009). We monitored seedling emergence weekly for 9 months (from January to September), recording the date that any seedling part first emerged from the substrate surface. At the end of the experiment (33 weeks after sowing), we measured the length of emerged seedlings and extracted them and separated the aboveground part (i.e., leaves), the underground part (i.e., root), and the seed. Both aboveground and underground parts were dried for 72 h at 50°C and weighed to determine dry biomass.

Statistical Analyses

Data on seedling emergence and seedling growth were analyzed through linear mixed models using the “lme4” package in Rstudio v. 1.1.383 (R Core Team, 2017). To analyze the final proportion of seedling emergence (or emergence success), we constructed generalized linear mixed models (GLMMs) with binomial error distribution (and associated logit link). To the response variable, the value “0” was assigned to those seeds that had no emerged and “1” when it did emerge. “Seed treatment” was the only predictor variable. To analyze seedling growth (using as response variables “Seedling length” and “Seedling dry weight”), we constructed linear mixed models (LMMs) with a gaussian error distribution, using as predictor variables “Seed treatment” and “Emergence time” (i.e., number of weeks between sowing and emergence). Due to the fact that seedlings developed either one or two leaves, three linear models were constructed for the response variable “Seedling length”: model 1 with the length of the first (i.e., the highest) leaf as response variable, model 2 with the additive length (i.e., the addition of the length of the two leaves), and model 3 with the absence or presence of the second leaf as a binomial distribution. Regarding the variable response “Seedling dry weight”, we constructed three linear models as well: model 1 with the aboveground dry weight, model 2 with the underground dry weight, and model 3 with the total weight. The variable “Study site” was included as random effect in all models. We fitted the GLMMs using Laplace approximation to maximum likelihood and the LMMs using restricted maximum likelihood (REML). Adjusted means and standard errors were calculated using the package “lsmeans”, as well as the contrasts among the different levels of significant main factors through a Tukey *post-hoc* test.

On the other hand, to assess the potential effects of the different treatments on the emergence rate (speed), we used failure-time analyses by fitting a Cox proportional hazard regression mixed model (Therneau and Grambsch, 2000) to data consisting of the number of weeks between sowing and

seedling emergence. To separate the effects on emergence rate from those on emergence success, we only considered seeds that had emerged by the end of our germination experiment (e.g., Fedriani et al., 2012). “Study site” was included as frailty factor. The significance of the target factor was evaluated by backwards stepwise elimination from the full model. In comparing successive models, we calculated the double absolute difference of their respective expectation maximization (EM) likelihood algorithms and compared that value against a chi-square with $k-1$ degrees of freedom, k being the number of levels of the factor being tested. For the frailty factor we also assumed a chi-square distribution with one degree of freedom (Therneau and Grambsch, 2000). For this purpose, we used the package “survival” in Rstudio v. 1.1.383 (R Core Team, 2017).

RESULTS

Quantitative Effectiveness: Seeds per Sample and per Distance

Overall, we collected 56 mammal samples, of which 17 belonged to goat (*Capra hircus* L.) samples (both spits and regurgitations, **Figures 3A,B**) and 39 were pine marten (*Martes martes* L.) feces (**Figure 3C**). A total of 203 seeds of *C. humilis* were recovered from the samples: 179 seeds from goat samples, specifically 99 regurgitated seeds and 80 spit out seeds, and 24 seeds from pine marten feces. Goat samples were present in three of four study sites, with a frequency of seed occurrence of 100%. Pine marten feces were found in all study sites, although the frequency of *C. humilis* seed occurrence was 50% in Cala Bóquer, 25% in Ermita de Betlem and 0% in the rest of the study sites (**Table S1**). Therefore, the mean number of samples that contained seeds per transect was 4.25 ± 1.65 for goat and 2.25 ± 1.65 for pine marten (**Figure 4A**). Regarding the number of seeds per sample, it was much lower for pine marten, 2.2 ± 1.8 , than for goat, 8.1 ± 3.6 (**Figure 4B**). The difference increases when considering the total number of seeds dispersed by each species (i.e., multiplying the number of samples with seeds by the number of seeds per sample), being 44.7 ± 19.7 for goat and 6.0 ± 3.7 for pine marten (**Figure 4C**). Finally, the total number of seeds dispersed corrected by the length (km) of each transect shows again that goats are much more important quantitatively (165.6 ± 138.5) than pine martens (9.5 ± 8.2) (**Figure 4D**). Specifically, 94.6 ± 79.8 seeds per km were regurgitated and 71.0 ± 58.8 seeds per km were spit out by goats.

Qualitative Effectiveness: Seedling Emergence

Overall, 43.45% of the sown seeds ($n = 290$) germinated. Treatment-specific final emergence percentages were, on average, $56.3 \pm 13.6\%$ ($n = 43$), $81.1 \pm 8.4\%$ ($n = 44$), $27.9 \pm 7.9\%$ ($n = 99$), $49.4 \pm 4.4\%$ ($n = 80$), and $63.3 \pm 3.3\%$ ($n = 24$) for control seeds with pulp, manually-depulp control seeds, seeds regurgitated by goats, seeds spit out by goats, and pine marten-ingested seeds, respectively. Nonetheless, if

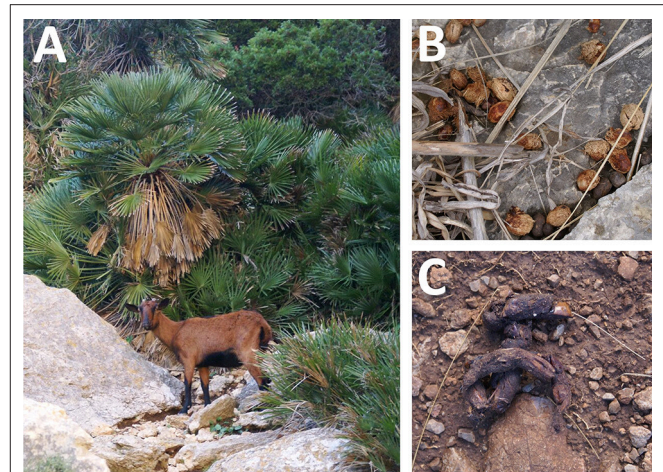
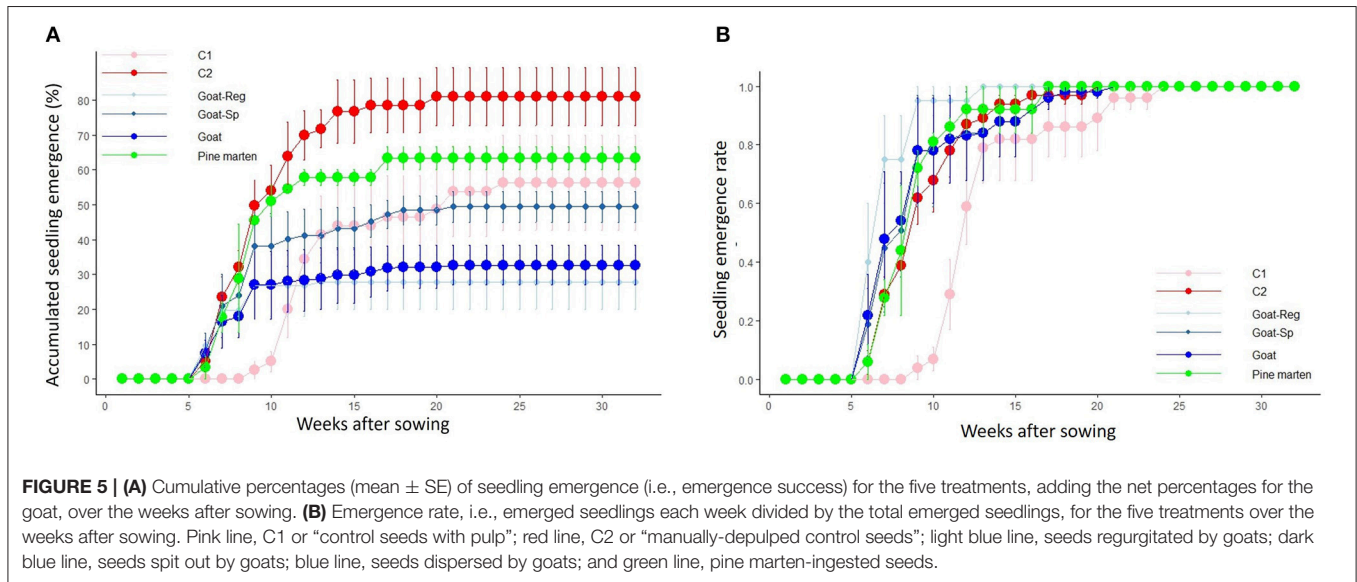
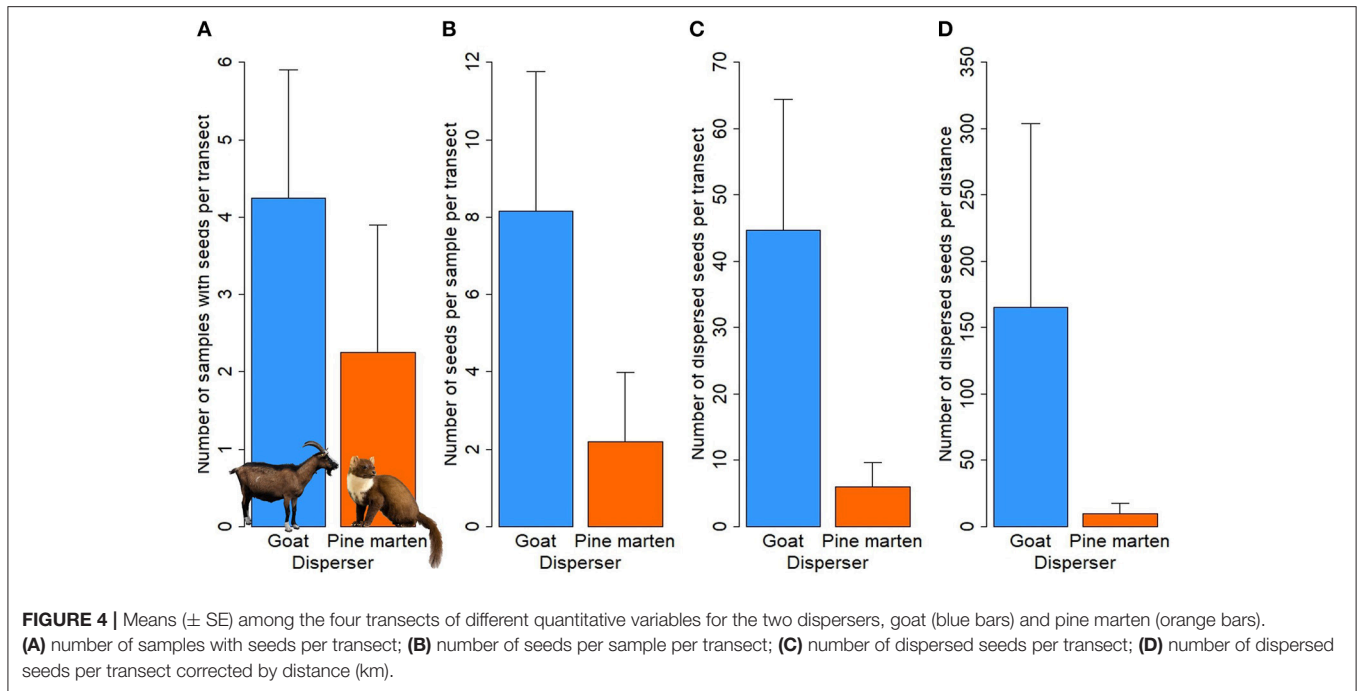


FIGURE 3 | Local mammal fruit consumers of *Chamaerops humilis* identified in the study. **(A)** A goat (*Capra hircus*) in front of several individuals of dwarf palm. **(B)** *C. humilis* seeds expeled by goat. **(C)** Pine marten (*Martes martes*) feces with *C. humilis* seeds.

we consider seeds regurgitated and spit out by goats together, the final emergence percentage of seeds dispersed by goats is $32.7 \pm 5.7\%$ ($n = 179$). Seedling emergence started 6 weeks after sowing (March 2018) for all treatments except for control seeds with pulp (C1), which started 3 weeks later (April 2018; **Figure 5A**). No seedling emerged in the last 8 weeks of monitoring. The Cox regression analyses indicated that, once corrected for the effect of study site (random or frailty factor), there were strong and significant differences among treatments in emergence rate ($\chi^2 = 29.43$, $df = 4$, $P < 0.0001$). Thus, on average, manually-depulp control seeds and pine marten-ingested seeds emerged 2.4 weeks earlier than control seeds with pulp. Seeds regurgitated and seeds spit out by goats emerged 5.0 and 3.3 weeks earlier than control seeds with pulp, respectively (**Figure 5B**). The hazard ratio of control seeds with pulp was <1 (0.4), which suggests that the presence of fruit pulp, and thus germination inhibitors, delayed seedling emergence.

Our mixed model revealed that seed treatment had a significant effect ($\chi^2 = 41.37$, $df = 4$, $P < 0.0001$) on final emergence success (**Table 2**), being highest for manually-depulp control seeds and lowest for seeds regurgitated by goats (**Figure 6A**). In pairwise comparisons (**Table S2**), differences were significant between control seeds with pulp and seeds regurgitated by goats, manually-depulp control seeds and seeds regurgitated by goats, manually-depulp control seeds and seeds spit out by goats, seeds regurgitated and seeds spit out by goats, and seeds regurgitated by goats and pine marten-ingested seeds. About 24.6% of mammal dispersed seeds collected in the field ($n = 203$) were predated by insects (i.e., they had at least one beetle exit hole). Specifically, 18.7% ($n = 80$) of seeds spit out by goats and 35.3% ($n = 99$) of seeds regurgitated by goats had between 1 and 4 holes made by scoli beetle, probably introduced (Rodríguez et al., 2014). No predated seeds were found for other treatments. To better understand the



relative qualitative effectiveness of seed dispersers in scenarios of absence of scolytine beetles, we ran the linear mixed model again but without considering scolytine-predated seeds. Results were very similar to the previous model, again with a significant effect of seed treatment ($\chi^2 = 28.14$, $df = 4$, $P < 0.0001$) on emergence success (Table 2), but differences were significant only in pairwise comparisons between each treatment and seeds regurgitated by goats (Table S2). Adjusted means of seeds regurgitated and spit out by goats were slightly higher in this case, but without substantial changes with respect to the other treatments (Figure 6B).

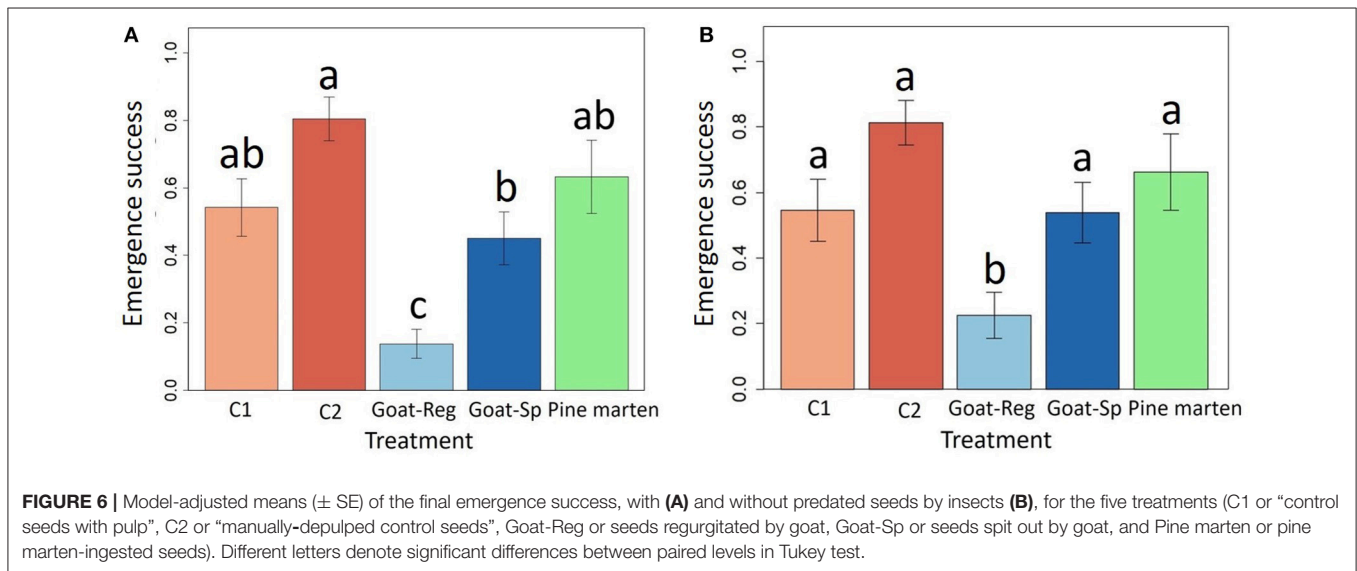
Qualitative Effectiveness: Seedling Growth

Once the study site effect was corrected for, our linear mixed models revealed that seed treatment only had a marginal effect on seedling length for the first (and largest) leaf ($\chi^2 = 8.74$, $df = 4$, $P = 0.07$; Table 3). However, emergence time had a significant effect on seedling length in the three models ($\chi^2 = 16.43$, $df = 1$, $P < 0.0001$), always reaching higher values those that emerged earlier. In order to evaluate whether the relationship between emergence time and seedling length was consistent among treatments, we fitted simple linear regressions using the length of the first leaf as variable. The correlation

TABLE 2 | Main results of the generalized linear mixed models testing the effects of emergence success, with and without predated seeds by insects (response variable), for each treatment (C1 or “control seeds with pulp”, C2 or “manually-depulp control seeds”, Goat-Reg or seeds regurgitated by goat, Goat-Sp or seeds spit out by goat, and Pine marten or pine marten-ingested seeds) (predictor variable).

Predictor variable	Seedling emergence			Seedling emergence without predated seeds by insects				
	χ^2	df	P-value	χ^2	df	P-value		
Seed treatment	41.37	4	<0.0001	28.14	4	<0.0001		
	Estimate	Standard error (SE)	Z-value	P-value	Estimate	Standard error (SE)	Z value	P-value
Intercept	0.17	0.34	0.48	0.63	0.18	0.39	0.48	0.63
Treatment C2	1.25	0.49	2.54	0.01	1.29	0.50	2.58	0.01
Treatment Goat-Reg	-2.00	0.47	-4.25	<0.0001	-1.42	0.47	-3.03	0.002
Treatment Goat-Sp	-0.37	0.43	-0.84	0.40	-0.03	0.44	-0.07	0.95
Treatment pine marten	0.38	0.54	0.70	0.48	0.49	0.55	0.88	0.38

Above, the results of Chi-square tests (χ^2 , DF, P-value). Below, the output of the model summaries [estimate, standard error (SE), Z value, P-value]. Treatment C1 acts as the intercept in these models. Significant differences ($P < 0.05$) are marked in bold.



was significantly negative for the whole dataset including all treatments and controls ($P < 0.0001$, **Figure S1A**) and for both control treatments “C1” and “C2” ($P < 0.0001$, **Figure S1B** and $P < 0.05$, **Figure S1C**, respectively). Nevertheless, it was non-significant for seeds regurgitated by goats, seeds spit out by goats, and pine marten-ingested seeds (**Figures S1D–F**), suggesting that seed processing by dispersers altered the negative relationship between emergence time and seedling length.

Seed treatment had a significant effect on seedling underground dry weight and total dry weight ($\chi^2 = 12.94$, $df = 4$, $P = 0.01$ and $\chi^2 = 10.29$, $df = 4$, $P < 0.05$, respectively), being highest for pine marten-ingested seeds and lowest for seeds spit out by goats (**Figures 7A,B**), but showed no effect on seedling aboveground dry weight ($\chi^2 = 4.89$, $df = 4$, $P = 0.3$; **Figure 7C**). In addition, emergence time had a significant effect on seedling aboveground, underground and total dry weight ($P < 0.01$; **Table 4**); seedlings emerging earlier showed higher dry weights. Pairwise comparisons through Tukey test

(**Table S3**) indicated that differences were significant between manually-depulp control seeds—seeds spit out by goats, and seeds spit out by goats—pine marten-ingested seeds for underground dry weight. However, for aboveground dry weight differences among seed treatments were non-significant. Finally, for total dry weight, differences were only significant between manually-depulp control seeds and seeds spit out by goats.

Total Seed Dispersal Effectiveness (SDE)

The SDE landscape shows that goats are, overall, about nine times more effective seed dispersers (SDE = 54.14) than pine martens (SDE = 6.03) (**Figure 8**). Goats are high-quantity and medium-quality dispersers, whereas pine martens are high-quality but low-quantity dispersers. Moreover, if goat-treatments are separated, seeds spit out are better qualitatively (SDE = 35.07) than seeds regurgitated (SDE = 26.4). The higher overall dispersal effectiveness of goats occurred even though some goat-processed seeds were predated by scolytines.

TABLE 3 | Main results of the linear mixed model testing the effects of seed treatment (C1 or “control seeds with pulp”, C2 or “manually-depulp control seeds”, Goat-Reg or seeds regurgitated by goat, Goat-Sp or seeds spit out by goat, and Pine marten or pine marten-ingested seeds) and emergence time (predictor variables) on seedling length for the first leaf (response variable).

Predictor variables	χ^2	df	P-value
Seed treatment	8.74	4	0.07
Emergence time	16.43	1	<0.0001

	Estimate	Standard error (SE)	t-value	P-value
Intercept	35.56	2.48	14.35	<0.0001
Treatment C2	0.10	1.48	0.07	0.94
Treatment Goat-Reg	-3.40	1.87	-1.82	0.07
Treatment Goat-Sp	-2.63	1.47	-1.78	0.08
Treatment Pine marten	0.23	1.85	0.12	0.9
Emergence time	-0.59	0.14	-4.05	<0.0001

Above, the results of Chi-square test (χ^2 , DF, P-value). Below, the output of the summary [estimate, standard error (SE), t value, P-value]. Treatment C1 acts as the intercept in this model. Significant differences ($P < 0.05$) are marked in bold.

DISCUSSION

Island systems are well-known to be fauna-depauperated and, consequently, to have highly specialized plant-animal mutualisms, such as plant-frugivore interactions (e.g., González-Castro et al., 2012). Therefore, past fauna extinctions may lead to important ecological consequences for plant communities on islands (Hansen and Galetti, 2009; Traveset and Richardson, 2014), like the functional replacement of the extinct seed dispersers by contemporary frugivore assemblages (e.g., Traveset, 1995; Celedón-Neghme et al., 2013). This study assesses for the first time the SDE for *C. humilis* on islands, and describes understudied dispersal systems, that is, goats (*C. hircus*) and pine martens (*M. martes*) as seed dispersers of this palm in the largest Balearic island. Moreover, this study contributes with a valuable example of how non-native species can be exerting an important ecosystem function that was likely lost thousands of years ago, when humans led to the extinction of the unique native mammals on many Mediterranean islands.

Quantitative Effectiveness

Our results indicate that the quantitative component of SDE was high for goats and low for pine martens. Several variables could be explaining these large differences between both species. First, the local abundance of the disperser is a relevant variable for SDE (Schupp et al., 2010). In this case, an extremely high abundance of goats has been reported in Mallorca (it is estimated that several tens of thousands live in the island—exact amount not known; Vives and Baraza, 2010). They are heterogeneously distributed throughout Serra de Tramuntana and Serra de Llevant (Bioatles—Govern de les Illes Balears²). Second, the number of fruits handled per visit seems to be much higher for goats than for pine martens, and the handling behavior could also influence on the final number of seeds dispersed per feeding bout. Given that humans are largely determining the number of goats

on Mallorca (Mayol et al., 2017), they are probably influencing the “relative seed dispersal effectiveness”, not only for *C. humilis*, but also for many other systems where livestock “rescues” the seed dispersal service of anachronistic plant species (Janzen and Martin, 1982; Cares et al., 2018).

Goats have been described to expel the ingested seeds while defecating (e.g., Mancilla-Leytón et al., 2011) or ruminating (e.g., Delibes et al., 2017a); however, we found no goat feces with *C. humilis* seeds in our study sites. On the other hand, introduced common genets (*G. genetta*) were scarce in the study area and no feces were found during the surveys; moreover, this species usually defecates in rather unsuitable sites for seed germination and seedling establishment (rocks and cliffs; Traveset, 2002). Likewise, we detected no signs of rabbit or rodents fruit consumption in our transects. We must note, however, that the sampling surveys were focused on forest tracks, which could be overestimating the quantitative contribution of some frugivore species—like the pine marten, which is known to use tracks to fecal marking (Barja, 2005) -, at the same time that we could have underestimated the contribution of others, like the common genet. On the other hand, pulp feeders (rabbits and rodents) could not have been identified through the fecal sampling surveys since they usually consume the pulp, leaving the seeds under the mother plant (Fedriani et al., 2012).

Qualitative Effectiveness

Seed dispersers can affect germination via two effects: (1) neutralization of the pulp inhibitory effect due to the removal of the pulp, and (2) seed coat scarification effect (Samuels and Levey, 2005). In our study, the earliest emergence of both manually-depulp control seeds and ingested seeds indicates that disperser species influence emergence time by removing the pulp inhibitory effect (Fedriani and Delibes, 2009). In relation to seed coat scarification, seed treatment in goat-stomach during rumination (i.e., digestive contractions and fermentation) could be accelerating seed germination as seed regurgitated by goats showed the highest emergence speed. However, this treatment is sometimes too harsh for seed viability, leading to the damage of seed embryos (i.e., seed predation) (e.g., Mancilla-Leytón et al., 2015; Jara-Guerrero et al., 2018) and, consequently, decreasing the final emergence success. Pine marten-ingested seeds showed the highest emergence success (after the manually-depulp control seeds); however, this disperser does not seem to be exerting any effect on emergence speed through seed scarification. Regarding seedling growth, seeds spit out by goats showed the lowest values of seedling dry weight, whereas pine marten-ingested seeds the highest ones. This could suggest that treatment in the mouth of goats could be more aggressive than treatment in the gut of pine martens, since chewing process is very intensive in ruminant species (Mancilla-Leytón et al., 2015). Nonetheless, the seedling dry weight of seeds regurgitated by goats was rather similar to that of pine marten-ingested seeds (Figures 7A,B), thus further research is required to go in depth in these results. In addition, it is necessary to consider that the method used to classify seeds regurgitated vs. seeds spit out by goats might be not entirely objective. As it is already known, seed treatment in mouth and gut differs between frugivore species

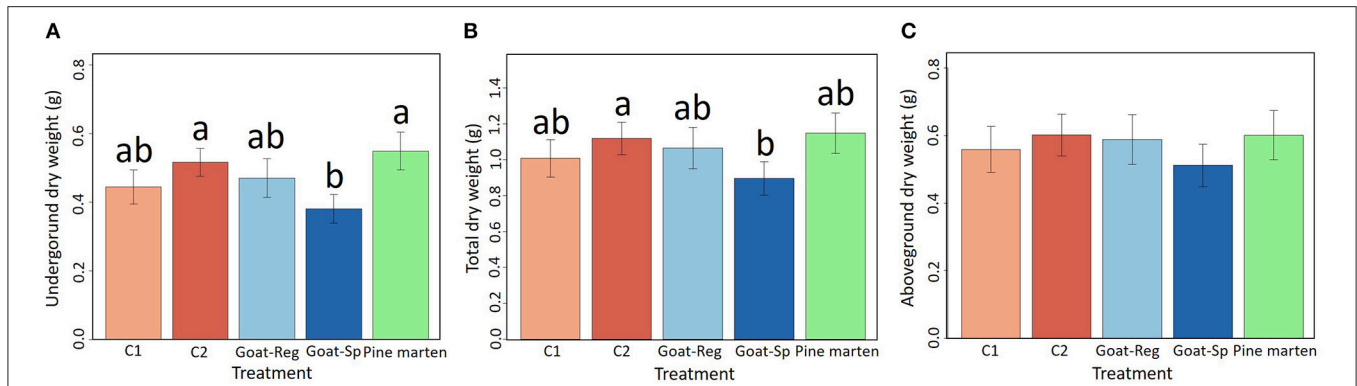


FIGURE 7 | Model-adjusted means (± SE) of seedling underground dry weight (A), seedling total dry weight (B), and seedling aboveground dry weight (C) for the five treatments (C1 or “control seeds with pulp”, C2 or “manually-depulp control seeds”, Goat-Reg or seeds regurgitated by goat, Goat-Sp or seeds spit out by goat, and Pine marten or pine marten-ingested seeds). Different letters denote significant differences between paired levels in Tukey test.

TABLE 4 | Main results of the linear mixed models testing the effects of seed treatment (C1 or “control seeds with pulp”, C2 or “manually-depulp control seeds”, Goat-Reg or seeds regurgitated by goat, Goat-Sp or seeds spit out by goat, and Pine marten or pine marten-ingested seeds) and emergence time (predictor variables) on seedling growth: aboveground, underground, and total seedling dry weight (response variable).

Predictor variables	Aboveground dry weight			Underground dry weight			Total dry weight		
	χ^2	df	P-value	χ^2	df	P-value	χ^2	df	P-value
Seed treatment	4.89	4	0.3	12.94	4	0.01	10.29	4	0.04
Emergence time	7.14	1	0.007	13.36	1	0.0002	13.28	1	0.0003

	Estimate	SE	t-value	P-value	Estimate	SE	t-value	P-value	Estimate	SE	t-value	P-value
Intercept	0.70	0.10	7.22	<0.0001	0.63	0.08	7.61	<0.0001	1.34	0.16	8.47	<0.0001
Treatment C2	0.04	0.05	0.80	0.42	0.07	0.05	1.40	0.16	0.11	0.09	1.20	0.23
Treatment Goat-Reg	0.03	0.07	0.44	0.66	0.03	0.07	0.40	0.69	0.06	0.12	0.50	0.62
Treatment Goat-Sp	-0.05	0.05	-0.90	0.37	-0.06	0.05	-1.23	0.22	-0.11	0.09	-1.22	0.22
Treatment Pine marten	0.04	0.07	0.63	0.53	0.10	0.06	1.62	0.11	0.14	0.11	1.22	0.22
Emergence time	-0.01	0.005	-2.67	0.0003	-0.02	0.005	-3.65	0.0004	-0.03	0.01	-3.64	0.0004

Above, the results of Chi-square test (χ^2 , DF, P-value). Below, the output of the summary [estimate, standard error (SE), t value, P-value]. Treatment C1 acts as the intercept in these models. Significant differences ($P < 0.05$) are marked in bold.

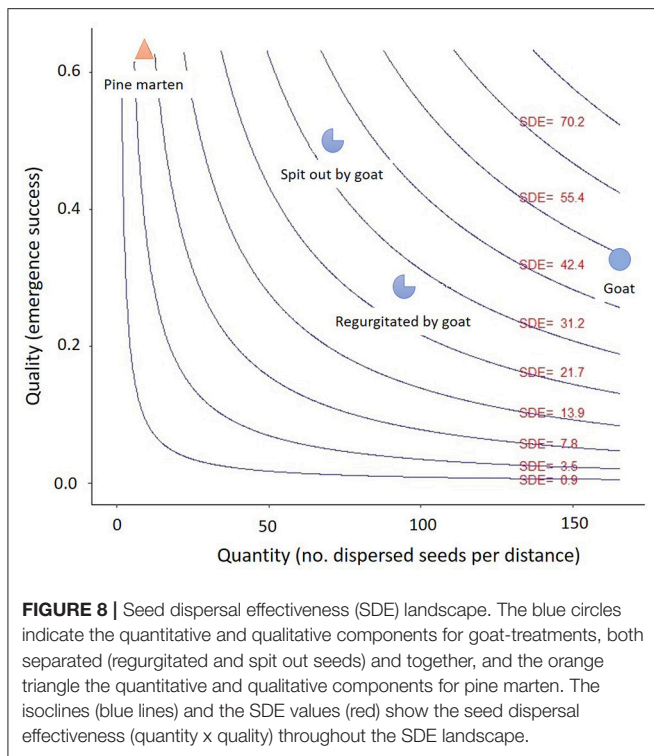
–and might differ as well among conspecific individuals– as a consequence of differences in morphological and physiological traits, as well as in retention times (Traveset et al., 2007). In conclusion, the monitoring of seedling emergence and seedling growth suggests a higher qualitative seed dispersal effectiveness for pine martens than for goats.

Frugivore-plant interactions can turn out into trade-offs, i.e., benefits and costs, for plant fitness (e.g., Fedriani and Delibes, 2011). Regarding the quality of seed deposition, all the seeds predated by scoli beetle found in the field had been dispersed by goats, specifically 18.7% ($n = 80$) of the seeds spit out and 35.3% ($n = 99$) of the seeds regurgitated. This might be related with seed covering, since pine-marten dispersed seeds are embedded in the dung (Traveset et al., 2007), but might also be due to persisting pulp surrounding the seed, which is probably higher for seeds spit out by goats and pine marten-ingested seeds than for those regurgitated by goats. Thus, pulp removal by frugivorous vertebrates appears to enhance germination,

but at the same time it represents a risk due to the cost of insect predation increase (Rodríguez et al., 2014). Moreover, seeds dispersed by goats are deposited in aggregates of ~8 seeds on average, and it is very likely that high seed density has a negative effect on seedling establishment by intraspecific competition (Murray, 1998). Finally, it is well-known that the microsite of seed arrival is a key qualitative aspect of seed dispersal effectiveness (García-Cervigón et al., 2018), so it must be considered in future studies where seedling emergence and survival are monitored under field conditions.

Total Seed Dispersal Effectiveness (SDE)

Overall, the relative contribution of goats to the seed dispersal effectiveness of *C. humilis* is more important than that of pine martens, mainly due to the quantitative component. Goat long-distance mobility, the great amount of fruits per time that they can consume, and a long seed retention time in the gut support



their functional relevance in many dispersal systems (Mancilla-Leytón et al., 2011; Grande et al., 2013). In Spain, goats have been shown to disperse effectively the seeds of at least 12 species, including *C. humilis* (Robles et al., 2005; Mancilla-Leytón et al., 2011, 2015; Delibes et al., 2017a). Pine martens also transport seeds over long distances (González-Varo et al., 2013; up to ~1,200 m) and have long retention times in the gut (Schaumann and Heinken, 2002). Moreover, they are known to consume many fleshy-fruited species in Northern Spain (Clevenger, 1993; Bermejo and Guitián, 1996; Rosellini et al., 2007), as well as *C. humilis* among other species in the Balearic Islands (Clevenger, 1995); however, the number of fruits per feeding bout is usually very low, and their population densities are not as high as those of goats.

We must consider, however, that goats not only act as effective seed dispersers, but also as herbivores, browsing frequently on *C. humilis* (Rivera Sánchez, 2014) and devastating leaves and inflorescences of many other plants (Mayol et al., 2017); and also as pre-dispersal seed predators (Mancilla-Leytón et al., 2011) like other ruminant species (e.g., Giordani, 2008). These ungulates have been reported to cause much damage on a number of plant species (Rivera-Sánchez et al., 2015), many of them threatened (Mayol et al., 2017). On the other hand, endemic plant species in Mallorca seem to have evolved under the selective pressure of herbivore ungulates (Vives and Baraza, 2010; Bover et al., 2016), and moderate browsing by goats indeed helps to maintain plant communities (Johnson, 2009; Rosa García et al., 2012). All these potential goat negative effects on other life plant stages of *C. humilis* as well as goat impact on other plant populations prevent considering them as necessarily positive from a conservation point of view.

Goat and Pine Marten: Surrogate Dispersers of *Myotragus balearicus*?

The extinct Balearic goat-like *Myotragus balearicus* Bate, the only medium-sized mammal present on the island in the Pleistocene, was a generalist species with a broad dietary niche, encompassing leaves, stems and inflorescences of diverse plant species (Bartolomé et al., 2011; Winkler et al., 2013a; Rivera et al., 2014; Welker et al., 2014). Several authors have suggested the pivotal role of this species as shaper of vegetation dynamics, acting as a keystone species in these insular ecosystems during the Pleistocene and Holocene (Palmer et al., 1999; Winkler et al., 2013b; Welker et al., 2014). Although no seeds have been found so far in any coprolites (Rivera et al., 2014; Welker et al., 2014), it is not discarded that *M. balearicus* could also feed on fruits (as many goats do today, e.g., Mancilla-Leytón et al., 2015; Delibes et al., 2017a) and discard seeds intact, thus acting also as a legitimate disperser. On the other hand, even though the origin of *C. humilis* in the Balearic Islands remains uncertain (Carrión, 2012), its old presence in the eastern coast of the Iberian Peninsula (Arroyo et al., 2004; Pérez-Obiol et al., 2010) would make more plausible the hypothesis of a Balearic existence before the recent human arrival. García-Castaño et al. (2014) even suggest that Balearic dwarf palm populations might appeared because of microplate migrations from the Oligocene or during the Messinian salinity crisis. In addition, an active human transport of *C. humilis* should have taken place along the Mediterranean basin in the Quaternary (García-Castaño et al., 2014; Guzmán et al., 2017).

Our study demonstrates that both goats and pine martens are effective seed dispersers of *C. humilis* in Mallorca, and we thus hypothesize that these introduced frugivores, especially the goat, could be replacing the function probably carried out by the extinct *M. balearicus* in the past, acquiring the role of seed dispersal “rescuers”. This role has already been suggested for the goat in other systems (e.g., Mancilla-Leytón et al., 2015; Cares et al., 2018). So, despite the fitness costs imposed by both introduced mammals, they could be providing an indispensable service to this ancient palm by dispersing it on island systems, where native dispersers are extinct and the alternatives are very limited.

CONCLUSIONS

In spite of the myriad negative impacts widely described for non-native species on islands (Reaser et al., 2007; Mayol et al., 2017; Rogers et al., 2017; Weller et al., 2018), their role as rescuers of ecological functions, lost in the past with fauna extinctions, acquires great relevance under the current scenario of increasing defaunation (Dirzo et al., 2014; Malhi et al., 2016). Our results here support the Janzen and Martin (1982) anachronism hypothesis and suggest that non-native species can disperse effectively anachronistic fruits, exerting a fundamental role in insular ecosystems. Thus, more studies are required to assess the role of non-native species in depauperated communities and to establish suitable management programs to preserve plant species and their associated ecological functions in Mediterranean ecosystems.

AUTHOR CONTRIBUTIONS

JMF and AT: experimental design and field work. RM-G and JMF: laboratory work. RM-G: statistical analyses and original paper draft. RM-G, JMF, and AT: paper review and editing.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00161/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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