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Interaction motifs variability in a Mediterranean palm under environmental disturbances: the mutualism–antagonism continuum

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The nature and the strength of plant–frugivore interactions often vary along an antagonism–mutualism continuum and are highly influenced by the local ecological context (e.g. level of environmental disturbances). However, little is known concerning how the local ecological setting where plant–frugivore interactions take place affects the seed dispersal effectiveness (SDE) and, eventually, plant recruitment. This knowledge gap relates to the scarcity of empirical investigations on individual-based plant–frugivore networks. We assessed whether the assembly of interaction modes (antagonist and mutualist) of the dwarf palm *Chamaerops humilis* (Arecaeae) affect the individual and the population level SDE in two Mediterranean sites differing in perturbation levels. We analysed the frequency distribution of interaction typologies and test its relationship with variation among individual palms in SDE. Additionally, we document how variation in interaction motif frequency (e.g. overrepresented interaction typologies) relates to changes in the SDE landscape of both disturbed study sites. We found that the interaction typologies of individual palms and its frugivores did not occur randomly. In a more complex landscape, interactions were more diverse and less dominated by simpler typologies, which may increase the stability of the plant–disperser interaction over the long term. We demonstrate that plants that interact with a more complex assemblage of frugivores, including both mutualistic and antagonistic partners, had the highest probability of recruitment. We found that the highly variable SDE among individual palms resulted from a few interaction modes occurring at higher than expected frequencies. We suggest this may be a reasonably frequent situation in diversified frugivore assemblages with a high heterogeneity of functional effects among mutualistic and antagonistic partners.

Keywords: context-dependency, disturbed habitats, frugivorous mammals, individual networks, plant–animal interactions, seed dispersal

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Introduction

For many centuries, the natural landscapes have experienced profound changes in land-use and fragmentation (Vernet 1990, Valladares et al. 2014), hunting, and defaunation (Rumeu et al. 2017) with negative consequences for ecosystem services (Forget and Jansen 2007). Interactions between plants and animals, which are the basis of the structure and functioning of ecosystems, are most vulnerable to those changes (Kissling and Schleuning 2015). For instance, biodiversity loss may disrupt seed dispersal interactions (Hansen and Galetti 2009, Pérez-Méndez et al. 2016), so that local extinctions of fruit-eating birds and mammals become major threats to the persistence of plant populations (Silva and Tabarelli 2000, López-Bao and González-Varo 2011). Declining plant populations may, in turn, negatively affect the populations of other seed dispersers, because fruits are critical food resources for many vertebrates (Jordano 2013).

Animal-mediated seed dispersal has advantages for plant populations such as reducing density and distance-dependent effects (Nathan and Muller-landau 2000) and the colonization of new habitats (Cain et al. 2000). These advantages are particularly strong when seedlings in different scenarios have very different chances of survival, e.g. after disturbance, or when density-dependent mortality near parent trees is extreme. In such circumstances, spatial heterogeneity in post-dispersal survival rates can have pervasive demographic impacts on plant populations (Howe and Miriti 2000). About 64% of gymnosperm and 27% angiosperm plant species produce fruits adapted for animal consumption (Herrera and Pellmyr 2002). The presence of rewarding fruits may attract functionally diverse mammalian frugivores, ranging from antagonists (e.g. seed predators) to mutualists (e.g. seed dispersers) (Chamberlain and Holland 2009, Schupp et al. 2017, Garrote et al. 2018). This leads to context-dependent fruit-removal rates and dispersal patterns, which are mediated by physiognomic plant characteristics, animal species, local habitat structure and anthropogenic disturbances (Carlo et al. 2007, Wehncke et al. 2009, Schupp et al. 2010, Perea et al. 2013). For instance, local abundance of dispersers affects interaction rates, where frequent visitors may act as poor dispersers or seed predators and infrequent visitors as the main legitimate dispersers (Fedriani et al. 2012, Sasal and Morales 2013, Simmons et al. 2018). Furthermore, the seed dispersal process is profoundly affected by the frugivores' ability to withstand anthropogenic disturbances (Elmqvist et al. 2003, García et al. 2013). Thus, understanding the factors that influence multispecies plant–frugivore assemblages, their local variation, and the effects on dispersal success is essential to assess plant population persistence in disturbed habitats (McConkey et al. 2012, Rost et al. 2012).

Few studies analyse networks that occur within a population, among individual plants and animals of several species interacting with them (Tur et al. 2015, Valverde et al. 2016, Rodríguez-Rodríguez et al. 2017). Moreover, previous analyses have largely ignored the combined interactions with both mutualistic and antagonistic partners that usually shape interaction outcomes among individual plants leading to contrasting pollination or seed dispersal success (Rodríguez-Rodríguez et al. 2017, Miguel et al. 2018). Thus, the combined effects of species partners that vary along the mutualistic–antagonistic gradient typically leads to the enormous diversity of interaction modes that characterizes marked context-dependency of the interactions (Rodríguez-Rodríguez et al. 2017, Miguel et al. 2018). The inherent, simultaneously positive and negative nature of all types of interactions has been largely ignored until recently (Gómez et al. 2019), with missing explicit analyses of situations where a specific pairwise interaction leads to variable outcomes depending on the spatial variation in biotic and abiotic conditions (Perea et al. 2013, Gómez et al. 2019). Individual-based networks analyse the interactions among individual plants based on the pattern of animals sharing, where each individual plant is considered a node, and is connected to conspecifics animals through an interaction event. This analysis provides a valuable approach to assess this variability of the outcomes by assessing variable interactions typologies at individual level (Gómez et al. 2019).

Recent work has shown that variation in interaction modes is significantly structured in natural populations, with distinct interaction motifs or interaction typologies that occur more frequently than expected at random (Milo et al. 2002, Jordano 2010, Simmons et al. 2018). It is virtually unexplored how these non-random interaction patterns at the individual level may add up and become drivers of the structure and dynamics of complex interaction networks at the community level (Stouffer 2010, Dupont et al. 2011). From this viewpoint, regularities in the marked context-dependency of plant–animal interactions (Bronstein et al. 2003) may emerge as variable, non-random, frequencies of interaction motifs. We might expect these variable patterns of interaction modes to shape local variation in seed disperser effectiveness resulting, for instance, in predictable shifts in the effectiveness landscapes (Schupp et al. 2017) in areas where disturbance regimes affect the composition of frugivore assemblages.

Our aims in this work are first, to evaluate if the antagonistic and mutualistic gradient of the frugivore interactions differ in environments with contrasting anthropogenic pressure. Second, to analyse if the interaction typologies at the individual plant level occur more frequently than expected at random (i.e. interaction motifs) in the population. Third, to evaluate how the frequency of interaction motifs characterises the changes in the seed dispersal effectiveness landscape (Schupp et al. 2010) in disturbed areas. Human-mediated disturbances may shift the frequency of interaction typologies from those with largely positive effects on dispersal success to others where interaction outcomes are detrimental for dispersal and regeneration. To answer these objectives, we empirically quantify the diversity of fruit–frugivore interactions of the estern European continental palm, *Chamaerops humilis*, whose local populations within the highly humanised Mediterranean basin, have experienced a recent and

extended process of fragmentation and reduction. This palm is an excellent model given the functionally-diverse assemblage of frugivorous mammals that consume its fruits in southern Spain (Fedriani and Delibes 2011). A variety of frugivores harvest *C. humilis* fruits, which include a quite unique coevolution where the species targets carnivorous animals to be legitimate seed dispersers. There are also pulp feeders (rabbits and rodents) and seed predators (ungulates) (Fedriani and Delibes 2011). Detailed documentation of the services provided by frugivores is limited for uncommon animal vectors, such as carnivorous mammals (Fedriani and Delibes 2009, López-Bao and González-Varo 2011) and ungulates (Perea et al. 2013). Thus, this study presents a first empirical attempt to quantify and characterise the combined antagonistic and mutualistic frugivory network at the individual plant level (Miguel et al. 2018).

Methods

Study species and area

The dwarf palm *Chamaerops humilis* is a small dioecious palm (Herrera 1989) relatively abundant in lowland Mediterranean scrub thickets and open pine forests. Fruits are attached to infructescences up to 30 cm long (1–142 fruits per ramet, mean = 25.7 ± 1.9) and located at 10–30 cm from the ground level. Fedriani and Delibes (2011) described the dwarf palm's main frugivores, mostly mammals. During the pre-dispersal phase European rabbits *Oryctolagus cuniculus*, cervids (*Cervus elaphus*, *Dama dama*), and up to six species of rodents (*Apodemus sylvaticus*, *Eliomys quercinus*, *Mus spretus*, *Mus musculus*, *Rattus rattus*, *Rattus norvegicus*; Kufner 1986) frequently prey upon the immature fruits (Herrera 1989, Fedriani and Delibes 2011). Fruits when ripened (early fall) smell strongly of rancid butter. This aroma attracts carnivorous mammals such as the Euroasian badger *Meles meles* and the red fox *Vulpes vulpes*, two effective long-distance seed disperser species (Fedriani and Delibes 2011). On the other hand, rabbits and rodents feed on the pulp of ripe fruits, generally performing seed dispersal over very short-distances by dropping the defleshed seeds underneath mother palms. Finally, ungulates like wild boars *Sus scrofa*, cervids (*Cervus elaphus*, *Dama dama*) and domestic goats *Capra hircus* generally prey upon the seed of the ripen fruits, acting as seed predators, but sporadically may spit out/defecate some seeds (Castañeda et al. 2017, Delibes et al. 2017, Muñoz-Gallego et al. 2019).

The study was carried out at two localities in the Doñana National Park (510 km²; 37°9′N, 6°26′W), on the right bank of the Guadalquivir estuary in southwestern Spain. We selected and delimited two plots (Matasgordas area = 22.1 ha, and Martinazo area = 21 ha) separated by 15 km within the Doñana area. During two consecutive fruiting seasons (October–November 2012–2013), we identified and tagged all the female palms with available ripen fruits (n = 70). Historically, both areas have been affected by intense human activities, such as defaunation, land use change and

periodical burnings (Granados et al. 1988). Both plots are within a dehesa, an agroforestry system characterized by the presence of a savannah-like open tree layer, mainly dominated by Mediterranean evergreen oaks. Matasgordas is a dehesa (ungrazed area) generated in 1970. It is characterised by a continuum of grasslands with an open tree stratum of *Quercus suber*, *Olea europaea* var. *sylvestris* and *Fraxinus angustifolia* and no, or only sparse, understory of Mediterranean scrubs (Fedriani et al. 2010). The area was used for intensive cow grazing until 1996, when the land became public and the cows were removed, under the protection of the Spanish National Park Service. Since then, the area became fully ungrazed and several mammal-dispersed plants, including *C. humilis*, are recolonizing the area (Fedriani et al. 2018). In this site, we monitored 46 females with ripe fruits. In contrast, the Martinazo dehesa (grazed area) is still used for livestock ranching (horses and cows), which increase the herbivory pressure over the native shrubs. Additionally, other woody species (*Q. suber*, *O. europaea* var. *sylvestris*) were cut down, and controlled rotating burnings were applied every 25–30 years (Granados et al. 1986, 1988). Since then, the area has been recolonized by vegetation composed mainly by a pyrophytic scrub (*Ulex* spp., *Stauracanthus* spp.) and *C. humilis* (Granados et al. 1988). Within this plot we monitored the ripe fruits of 24 females.

Frequency of visitors and fruit harvesting

To assess the relative relevance of frugivorous species, we examined the extent of variation among them in the frequency of visits to fruiting dwarf palms and the relative number of seeds handled by each species (i.e. quantity of seed dispersal; Schupp 1993, Jordano and Schupp 2000). We estimated fruit removal rates and the number of visits per day during the fruit ripening over two dispersal seasons (September–November) of 2012–2013. The dwarf palm fruit removal takes place on fruits still attached to the infructescence (Fedriani and Delibes 2011). We selected one or two infructescences per target female; fruits were counted at the start of the monitoring period and then every morning for twelve consecutive days each season. Thus, we estimated the difference in number of fruits between days and related to the frugivore visitors. We assessed the frequency of visits by different frugivores by estimating the number of visits at plant level in the 70 dwarf palms (in all, 1886 fruits monitored on plants). Visitor identification and an estimate of relative visitation rates were achieved through identification of their footprints in a semi-circular plot of a sandy substrate (1 m diameter) surrounding the infructescences (Mendoza and Dirzo 2007, Fedriani and Delibes 2013, Peris et al. 2017). When more than one species had visited a dwarf palm on the same day, the identity of the fruit remover was questionable. Therefore, we considered only those visits made by single visitors, for which identification of the fruit removal agent was conclusive (Fedriani and Delibes 2013). The footprints were cleaned at the start of each 12-day field experiment and again after each observation. Thus, visitation rate was estimated as no. of records in 12 days.

Frugivore effectiveness

We classified the interacting animals into two broad functional categories based in Fedriani and Delibes (2011) (also see Perea et al. 2013): mutualists (including both defleshers: rodents, rabbits and legitimate dispersers: badgers and foxes), and antagonists (seed predators: wild boars and cervids). Defleshers typically ingest the pulp of fruits, dropping the seed in situ or taking it over short distances, sometimes preying upon the seed itself. Legitimate seed dispersers swallow the fruits whole and defecate viable seeds; we have no evidence of seed cracking by these species. Antagonist typically crack open the seeds yet they may disperse some seeds intact. Yet these two categories are not mutually exclusive, and dwarf palm frugivores actually can be located at some position between these two extremes (Fedriani and Delibes 2011). To fully account for this variation, for each plant, we first defined the fruit removal effectiveness as the quantity component of seed dispersal effectiveness (no. of records multiplied by the number of fruits disappeared record^{-1}). This quantity component (QTY hereafter; Schupp et al. 2010), indicates the amount of fruit removed by frugivores.

To estimate the quality component (QLY, hereafter) we compiled available data from previous works on *C. humilis* seed dispersal in the Doñana National Park made in open areas in dehesa (Fedriani and Delibes 2011, Perea et al. 2013, Suárez-Esteban et al. 2013, Jácome-Flores et al. 2016, Castañeda et al. 2017) regarding: 1) fruit handling and fruit processing behaviour; 2) seed germination of handled and defecated/regurgitated seeds; and 3) probability of seedling survival. The cumulative probability is calculated from the product of the three probabilities: i.e. the successive probabilities that a fruit handled results in a removed seed; that a removed seed germinates after dissemination by the frugivore; and that a germinated seed ultimately results in an established seedling. Both sites are in a dehesa with similar vegetation cover, sandy substrate and microclimate conditions, thus, we assumed that the probability of seedling survival component was similar between sites. These estimates result in a cumulative probability of early seedling recruitment resulting from a fruit removal–dispersal event by each frugivore species, a useful proxy of their QLY component (Supplementary material Appendix 1 Table A3 for detailed information of each frugivore species). Fedriani and Delibes (2011) reported that the seeds ingested by badgers left in open space away from conspecifics resulted in a cumulative probability of early seedling recruitment (QLY) of 0.179.

We assumed that the seeds dispersed by foxes (left usually in open areas) had the same QLY value. For rabbits and rodents QLY (0.286) we used the results of seedling survival from hand-defleshed seeds sowed beneath fruiting plants obtained by Suárez-Esteban et al. (2013). Using seeds with manually-removed pulp mimics the effect of rabbits and rodents feeding behaviour and fruit manipulation (without ingestion), which left the defleshed seeds underneath mother palms. For antagonists, we estimated only the quantitative component of the effectiveness of each animal species, because we assumed that

all consumed seeds were destroyed during the chewing process and did not result in established seedlings. In wild boars, all seeds were assumed to be destroyed during chewing process, thus, we set QLY to 0. In contrast, a proportion of seeds consumed by cervids can be spat or vomited, and hence, dispersed. Therefore for cervids we set QLY to 0.011, which corresponds to the proportion of surviving regurgitated seeds reported by Castañeda et al. (2017).

For each individual plant we estimated the interaction strength for each frugivore species as a result of the combined strengths of all its visit records. For mutualists, we estimated the strength of interaction (SI) by multiplying each species fruit removal efficiency (QTY) by the estimate of the cumulative probability of early seedling recruitment resulting from their dispersal activity and fruit/seed processing behaviour and the effects on seed germination (QLY). Thus:

$$SI_P = [QTY_P] \times [QLY_P] \text{ where,}$$

$$SI = \big[\text{no. feeding records plant} \times \text{no. fruits}$$
$$\text{disappeared record}^{-1} \text{ plant} \big]$$
$$\times \big[\text{prob. of seed germination by frugivore}$$
$$\times \text{prob. seedling survival by frugivore} \big]$$

Finally, we defined the overall mutualistic interaction strength for each palm as the sum of its SI values with rabbits, rodents, badgers and foxes, and the overall antagonistic interaction strength as the sum of interaction values with wild boars and cervids. Low abundance of fruiting plants or logistic limitations prevented us from analyzing the two fruiting seasons separately; therefore, we analyzed all data over a pooled data set comprising both fruiting seasons.

Interaction motifs

To identify the interaction typology, we followed the methodology proposed by Rodríguez-Rodríguez et al. (2017). Based on the estimated interaction strengths, we characterized a quantitative version of the three-wise interaction typologies: each plant node (*P*) linked to a mutualistic (*M*) and/or an antagonistic (*A*) animal node, with the link values representing the summed interaction strengths of the individual palm with its *M* and *A* partner species (Fig. 1A). First, we generated an adjacency matrix based on the interactions between our group of 70 plants (*P*) and the two functional groups of animals, i.e. mutualists (*M*) and antagonists (*A*). Elements of this matrix (a_{PM} or a_{PA}, corresponding to the summed interaction strengths with *M* or *A* species for each plant) take values greater than 0 whenever any plant–animal interaction was recorded, and 0 in any other case. Any non-zero interaction thus resulted in some outcome in terms of fruit removal effectiveness We used the median of the corresponding frequency distribution of interaction strength(s) to
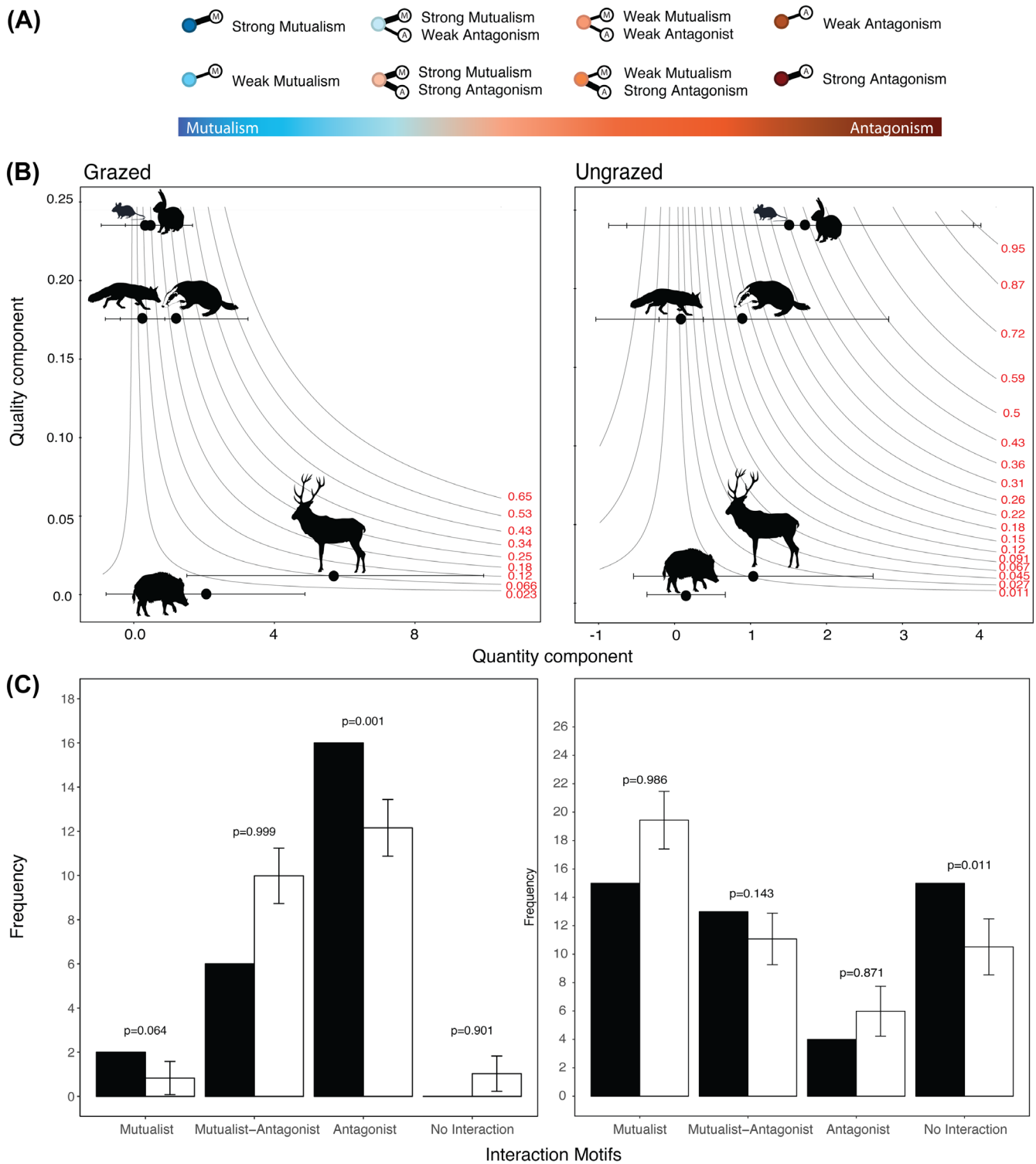
Figure 1. Typologies of interaction motifs for *Chamaerops humilis*–frugivore interactions in the study areas. (A) The different typologies illustrating the variation in interaction strength with mutualists (*M*) and antagonists (*A*) depending on the distribution of weak and strong interactions recorded for the plant in a colour gradient. Thick lines indicate strong interactions, while narrow lines depict weak interactions. (B) Effectiveness landscapes illustrating the locations of different frugivore species on the effectiveness landscape defined by both the quantity (QTY, x-axis) and the quality components (QLY, y-axis) of seed dispersal effectiveness. (C) Frequencies of interaction motifs observed (black bars) in the two study areas compared to their expected frequencies (white bars) obtained by randomising the individual-based networks of each area. Mean ± 1 SD is represented for expected values. p-values were obtained from upper-tailed Z tests (α = 0.05).

categorize the value as 'weak' (a_{PM} or $a_{PA} <$ median) or 'strong' (a_{PM} or $a_{PA} \geq$ median). Second, we deconstructed the network in its constituent subgraphs (M–P–A ternary subgraphs, Fig. 1A) to classify patterns of interaction based on interaction modes of the individual palms. These patterns were represented as undirected, weighted subgraphs of three nodes (M–P–A triads), where each node was an interaction partner (i.e. individual plant, combined mutualists and combined antagonists), the links between P and A–M nodes illustrating the interaction strength between the plant and the respective animal group. The deconstruction resulted in nine possible interaction modes from the 3×3 combinations of mutualistic and/or antagonistic interactions for each palm: individuals that only interact with mutualists, plants with strong-mutualistic and weak-antagonistic interactions, plants with weak-mutualism and weak-antagonism to plants that interact only with antagonists (Fig. 1A). However, due to the small sample size for several of the resulting typologies, we grouped them in four categories: 1) mutualistic (plants only with mutualistic interactions; weak/strong), 2) mutualistic–antagonistic (plants with both mutualistic and antagonistic interactions; all four combinations of weak/strong grouped), 3) antagonists (plants only with antagonistic interactions; weak/strong) and 4) plants with no interaction recorded (Fig. 1A).

Data analysis

We compared the potential contribution of each frugivore species to the seed dispersal of *C. humilis* in the two study sites through effectiveness landscape plots (Schupp et al. 2017). These plots are two-dimensional representations of each frugivore species interacting with the plant based on their fruit removal efficiency (QTY) and QLY (quality component; see interaction motifs section) (Fig. 1B) (Schupp et al. 2010, 2017). On each plot, the seed dispersal effectiveness is represented with isoclines with all combinations of QTY and QLY that result in the same values. For the resulting plots, we used the R-package effect.lndscp (Jordano and Rodríguez-Sánchez 2017; <https://github.com/pedroj/effectiveness_pckg>).

To test if each of the interaction typologies appears more frequently than expected in a random network (i.e. an interaction motif) of the same size, we generated 10 000 random networks based on the three alternative states of plant–animal interaction strengths (absent, weak, strong) keeping the probabilities of each one with the actual, observed values in our study plots. The resampling reshuffles interactions for the individual plants while keeping the overall interaction frequency with each partner species recorded in each population. Each random network is thus a bootstrap sample of the interaction network and equal in size, including a subset of plants (resampled with replacement) and their interactions (resampled from their actual distribution frequency). The motif counting algorithm explores each sampled network and tallies all the occurring interaction typologies to obtain their expected frequencies. Then, the distribution of the expected frequencies of each interaction motif is compared to the observed frequency using means of the one-tailed z test.

We used a series of plant traits (e.g. size, neighbourhood, aggregation level, density, number of infructescenses and fruiting synchroyny) to characterize each palm physiognomy and its potential relation with the interaction motifs; these traits (Supplementary material Appendix 1 Table A1) summarized potential characteristics mediating in frugivore visitation (Miguel et al. 2018). We used discriminant analysis to find a linear combination of traits that maximized the variation among palms with distinct interaction motifs. Traits that, when combined with others, provided the best discrimination power were selected through the Wilk's lambda criterion, using the greedy.wilks function from klaR package (Weihs et al. 2005, Heino et al. 2015). All independent variables were standardized ([variable − mean]/standard deviation) before analyses.

To test for the consequences of frugivores interactions on seed dispersal effectiveness (SDE), we used a linear mixed model, using the mean strength of interaction (SI) as the response variable. We included as predictors both the type of interaction motif associated with each plant and the standardized plant traits. As a random factor we used the study plot. Finally, we tested for differences in dispersal effectiveness among interaction motifs by post hoc pairwise comparisons (Hothorn et al. 2008). All analyses were performed in R (<www.r-project.org>).

Results

Frugivore visitors and seed dispersal effectiveness

We found frugivore tracks in 90% of dwarf palm individuals (n = 70 plants), with seven unvisited plants during both seasons in both plots. We recorded 425 visits, 97.9% were performed by single frugivore species/day/plant: 43.03% performed by cervids and 29.81% rabbits, followed by rodents with 12.98% and wild boars 6.73%. Carnivores were infrequent visitors, with badgers comprising 5.53% and foxes with only 1.92% of visits being recorded. Regarding fruit removal, from 1967 monitored fruits, 71.32% of them (n = 1403 fruits) were harvested in the following way: 52.21% by cervids, 17.43% rabbits, 13.35% rodents, 9.14% badgers, 6.75% wild boars and 1.12% by foxes (more details in Supplementary material Appendix 1 Table A3).

Overall, the fruit removal effectiveness resulted in marked differences among frugivore species in strength of interaction in both plots: we found that cervids are the more avid consumers (2.65 ± 0.13 fruits visit^{-1}), followed by rabbits (1.26 ± 0.08 fruits visit^{-1}), rodents (1.14 ± 0.09 fruits visit^{-1}), badgers (1.01 ± 0.08 fruits visit^{-1}), wild boars (0.80 ± 0.07 fruits visit^{-1}) and finally foxes (0.14 ± 0.02 fruits visit^{-1}).

The patterns of frugivore seed dispersal effectiveness were highly contrasting in the two plots studied (Fig. 1). Animals SDE was lower in the grazed area (0.23–0.65) compared with the SDE in the ungrazed area (0.011–0.95). Most changes in the SDE landscapes between the two areas were associated with shifts of the QTY component for the seed predators

Table 1. Frequency of interaction typologies and percentage of individual plants belonging to each typology.

| Plot | Interaction typology frequency | | | |
	Antagonist	Mutualist	Mutualist–antagonist	No interaction
Grazed	16 (66.67%)	2 (8.33%)	6 (25%)	0
Ungrazed	3 (6.52%)	15 (32.61%)	13 (28.26%)	15 (32.61%)

Pearson's χ^2 test = 32.73, df = 3, p < 0.0001.

wild boar and cervids (more abundant in grazed area) and for defleshers (highly abundant in the ungrazed area). Cervids and foxes reduced their effectiveness in more than one-order of magnitude, and badgers were 1.13 less effective than those in the grazed area. Both badgers and red foxes showed consistent values through locations, yet with overall SDE higher at grazed area. In the grazed area antagonism prevails, with effectiveness landscapes shaped by the quantity component. Specifically, we found that foxes in both had the lowest contribution to seed dispersal (0.01–0.04). At the plot level, badgers in the grazed area had the highest SDE (0.2), followed by the rabbits (0.1) and with similar values rodents and cervids (~0.07). Instead in the ungrazed area, rabbits and rodents had the highest SDE (0.43 and 0.36 respectively), followed by badgers (0.15) and, cervids and foxes with the lowest non-zero SDE (0.011).

Interaction motifs

The frequency of the interaction typologies differed significantly among localities (Table 1; χ^2 = 32.73, p < 0.001). In the grazed area, we found that 66.67% of the plants interact only with antagonists, being the dominant interaction typology followed by those plants that interact with both mutualists and antagonists (25%) and finally the less frequent interaction typology was the plants that interact only with mutualists (8.33%). In contrast, in the ungrazed area we found that, apart for 32.61% of the plants without interactions, the dominant interaction typology included plants that interact only with mutualists (32.61%), followed by the plants that interact with mutualists and antagonists (28.26%) and plants that only interact with antagonists (6.52%). We found that some of these interaction typologies were overrepresented, i.e. motifs (Fig. 1C). For instance, plants at The grazed area interacted more frequently than expected by chance with the antagonists (Z = 3.01, p = 0.002) and marginally with just the mutualists (Z = 1.54, p = 0.061). In ungrazed area, visited plants without records of disappeared fruits (no interaction), appeared more frequently than expected by chance (Z = 2.33, p = 0.010). Also, plants where both mutualists and antagonists interacted occurred more frequently than expected (Z = 1.70, p = 0.046).

A linear discriminant analysis (Table 2) showed that except from size (Wilk's λ = 0.722, F = 8.48, p < 0.001) plant traits are not good predictors for interaction modes classification, explaining just 40% of the variance in interaction mode. The two first discriminant functions explained 93.47% of variation among plants in traits (Supplementary material Appendix 1 Table A1) associated with interaction modes. The first discriminant function (LD1) showed that plants visited by antagonists were those with large size and a high number of inflorescences. The equiprobability ellipses of the core group of plants unvisited and visited by mutualists overlapped with the ellipse containing the plants visited only by the antagonists. The second discriminant function (LD2), mainly determined by spatial aggregation and neighboring effects, showed that the interaction modes (mutualist–antagonist, antagonist and no interaction) were not related to the plants spatial distribution.

Effect of interaction motifs on dispersal effectiveness

Variation in seed dispersal effectiveness across plants was significantly related with their interaction typologies even when statistically controlling for the plant traits, which did not have a significant effect (Table 3).

Through pairwise contrasts (Table 4) we found that plants interacting with both mutualists and antagonists were significantly different and higher in their seed dispersal effectiveness from plants that interact only with the antagonists (p = 0.006)

Table 2. Plant traits loading on the first two (LD1, LD2) linear discriminant functions, estimated with the greedy Wilk's function. Bold text indicates that variable have a significant effect p <0.05.

Variable	LD1	LD2	Wilk's λ	p-value
% Variance	72.14%	21.33%	–	–
Size	**−0.7104**	**0.3087**	**0.722**	**<0.001**
Neighbouring	0.2277	−0.6422	0.681	0.287
Clustering	0.2000	0.5988	0.637	0.226
Density	−0.0838	0.3727	0.561	0.853
Fruits/infructescence	0.1185	0.2259	0.610	0.427
No. of infructescences	−0.5978	0.0116	0.596	0.701
Fruits/plant	0.3300	0.1865	0.580	0.647
Synchrony	−0.1648	−0.0894	0.568	0.734

Table 3. Results of model fit with mean effectiveness as response variable (across frugivore species visiting a palm), with quasibinomial distribution with locality and standardized plant traits. Bold text indicates that variable have a significant effect p <0.05.

Effect	Estimate ± SE	t-value	p-value
Intercept	$-1.08 \times 10^{-04} \pm 0.007$	−0.015	0.988
Typology: mutualist	$7.65 \times 10^{-03} \pm 0.010$	0.742	0.462
Typology: mutualist–antagonist	$\mathbf{3.25 \times 10^{-02} \pm 0.010}$	**3.268**	**0.002**
Size	$-2.71 \times 10^{-03} \pm 0.005$	−0.516	0.609
Neighbouring	$4.19 \times 10^{-04} \pm 0.004$	0.098	0.922
Clustering	$-5.11 \times 10^{-03} \pm 0.004$	−1.221	0.229
Density	$-4.04 \times 10^{-03} \pm 0.005$	−0.830	0.411
Fruits/infructescence	$-5.56 \times 10^{-03} \pm 0.005$	−1.048	0.300
No. of infructescences	$4.05 \times 10^{-04} \pm 0.007$	0.061	0.951
Fruits/plant	$2.82 \times 10^{-03} \pm 0.007$	0.397	0.693
Synchrony	$7.63 \times 10^{-04} \pm 0.005$	0.153	0.879
Random effect: plot	1.541×10^{-06}		

and mutualists (p = 0.032) in all pairwise contrasts. However, plants with only one type of interaction (only mutualists/only antagonist) showed no differences in their dispersal effectiveness (p = 0.740) (Table 4).

Considering all the interaction typologies together for both plots, plants that interact with both groups of frugivores (mutualist–antagonist) had the highest values of seed dispersal effectiveness as observed in the top-right isolines (Fig. 2). In the grazed area, even though plants mostly interacted with antagonist had a SDE higher than those in the ungrazed area, where mutualist interactions were more abundant.

Discussion

Seeds dispersed efficiently is essential to assure the persistence of plant species in fragmented and disturbed landscapes. An immediate effect of deforestation is the loss of reproductive plants, potentially leading to situations of severe source limitation of seed dispersal (Muller-landau et al. 2002); yet a more pervasive effect is the accompanying loss of frugivores able to move the seeds and escape scenarios of dispersal limitation (seeds are available, but functional frugivore species that disperse them are missing). A variety of factors ensure that the process of seed dispersal remains functional even in situations of severe disturbance, including the visitation frequency of frugivores, the frugivores behavior and the number of seeds handled and dispersed (Schupp et al. 2010). Shifts in any of those components of SDE may cause either a collapse of the dispersal process (Pérez-Méndez et al. 2016), or replacement of dispersal services and compensatory effects by other frugivore species (Albrecht et al. 2013, Bueno et al. 2013, Polak et al. 2014).

By focusing on individual-based plant–frugivore interaction networks, our study presents a first attempt to understand how these interactions differentially occurred and structured their outcomes on plant dispersal effectiveness.

Frugivore visitors and seed dispersal effectiveness

Our results were consistent with previous reports of the functional roles of dwarf palm frugivores presented by Fedriani and Delibes (2011) and Castañeda et al. (2017). Dwarf palm frugivores differed in their fruit removal efficiency and dispersal quality, contributing to the overall plant recruitment in different proportions and modes. Given that these differences occur along a continuum between entirely antagonistic and fully mutualistic extremes (Perea et al. 2013, Gómez et al. 2019), variation in visitation pattern among plants and populations led to marked changes in interaction outcomes. The differences among species were dependent on the compensatory effects of the quantity and quality components of effectiveness, i.e. limited interaction frequency (visitation) compensated with higher per capita effects, and vice versa (Calviño-Cancela and Martín-Herrero 2009). Frugivore abundance has been proposed as a major factor that impinges the frequency of fruit–frugivore interactions (Burns 2006) by driving visitation frequency. However, regarding seed dispersal, it seems that frugivore abundance and seed dispersal quantity component are not necessarily correlated, as demonstrated by Perea et al. (2013), especially in situations of fruit resource use shifting related to the local abundance of alternative food sources. Furthermore, we found that the sporadic seed dispersal events performed by cervids had important consequences on local seed dispersal. Thus in the ungrazed area, even though mutualists were more frequent, overall

Table 4. Pairwise post hoc contrasts in seed dispersal effectiveness values between interaction typologies. Bold text indicates that variable have a significant effect p <0.05.

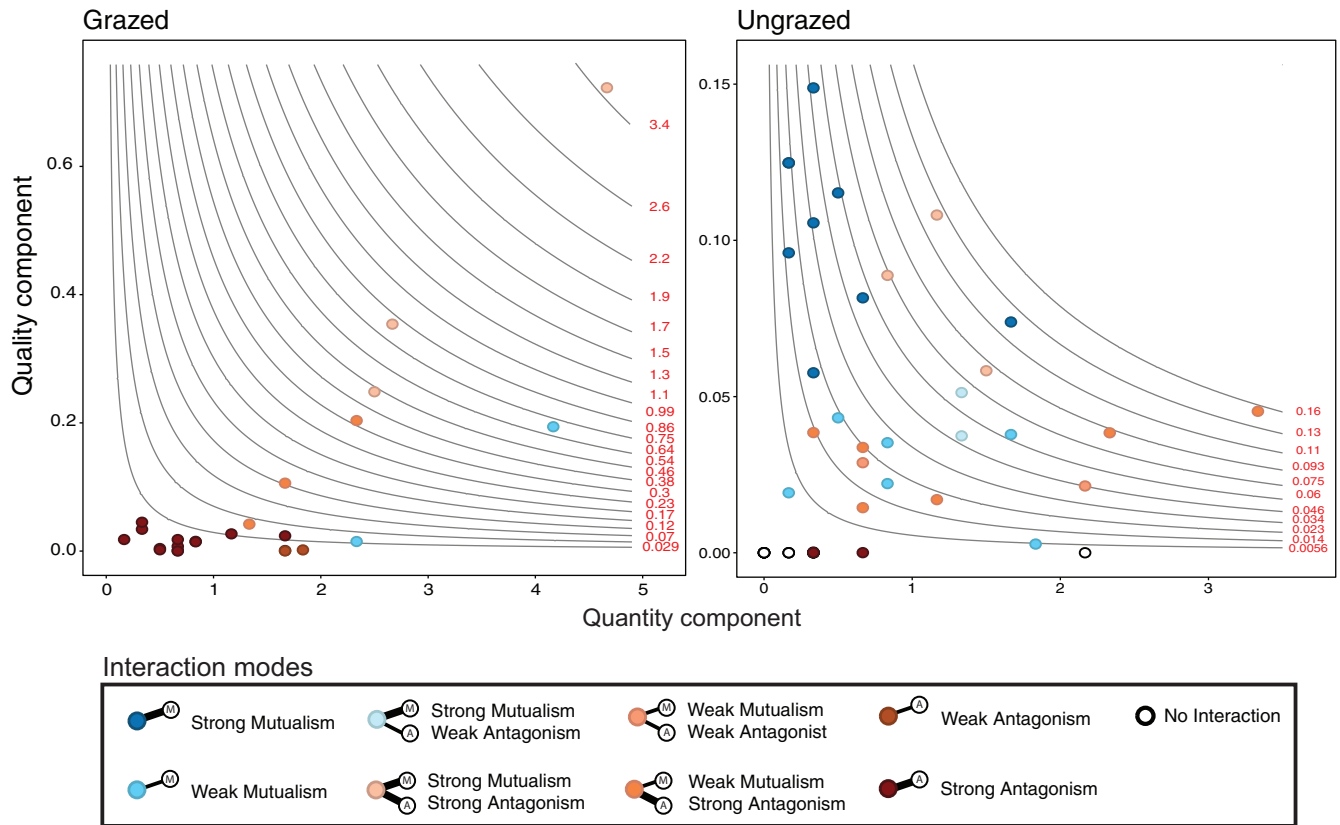|	Estimate ± SE	t-ratio	p-value
Mutualist versus Antagonist	$7.65 \times 10^{-3} \pm 0.010$	−0.742	0.740
Antagonist versus Mutualist–antagonist	$\mathbf{3.25 \times 10^{-2} \pm 0.010}$	**−3.268**	**0.006**
Mutualist versus Mutualist–antagonist	$\mathbf{2.49 \times 10^{-2} \pm 0.010}$	**−2.624**	**0.032**

Figure 2. Locations of different *Chamaerops humilis* plants from the two study sites on the effectiveness landscapes defined by the quantity and the quality components of seed dispersal effectiveness. Colors code groups of plants belonging to the same interaction typology (Fig. 1A).

effectiveness was lower because they could not compensate lower visit rates of inefficient but avid consumers.

Comparing our study plots, we found that the way interactions with frugivores is structured differed between the grazed and the ungrazed area, where the strength of interaction is not fully explained solely from differences in the frugivores' densities. We found that cervids, badgers and foxes were very abundant in the ungrazed area (Supplementary material Appendix 1 Table A2; rodents were excluded due to lack of information) but had a lower efficiency as seed dispersers than in the grazed. There are two interrelated processes that can explain the differences: frugivore satiation (Hampe 2008) and the presence of alternative food resources (Carlo et al. 2003, Russo et al. 2006). The ungrazed area had not only more dwarf palms than the grazed, but also is surrounded by undisturbed vegetation with a high density and diversity of fleshy-fruited species (mean $1856.7 \pm$ SE 7.59 ind·ha^{-1}; Garrote et al. 2018). Higher availability of food resources could promote shifts in major fruit food use, resulting in decreased fruit removal and seed dispersal services for dwarf palms in the ungrazed area, especially for cervids and badgers (Jordano 1987, Garrote et al. 2018). In contrast, in the grazed area, almost all woody species were cut down and the area and surroundings has been recolonized by vegetation composed mainly by pyrophytic scrub (Granados et al.

1988). Within this pyrophitic scrub, *Chamaerops humilis* (with some sparse *Olea europaea* var. *sylvestris* and *P. bourgaeana*) concentrates the most abundant food resource for frugivore mammals. This could explain the increased quantity component and interaction strength in both antagonist and mutualists interactions in this grazed area. These compensatory trends are analogous to those recently reported by Miguel et al. (2018) comparing grazed versus ungrazed habitats; they found that frugivores visit fewer trees in more structurally-complex habitats compared with trees in a more disturbed and physiognomically-simplified habitat.

Because our study uses a natural experiment instead of a controlled manipulation, we cannot exclude the influence of other factors explaining this variation in effectiveness. Similar shifts in SDE landscapes among localities are expected for other plants with mixed frugivore assemblages, where human-created disturbances can pervasively alter the frequency of visitation and/or frequency of fruit use and thus local population regeneration (Bueno et al. 2013).

Interaction motifs

We found a large variation in the relative frequencies of different interaction modes and the resulting interaction motifs among localities. For instance, individual plants at the grazed

area frequently showed mixed interaction modes involving interactions with both mutualists and antagonists; we found two overrepresented interaction typologies (antagonist and mutualists), both with a single functional group. Furthermore, most palm–frugivore interactions at grazed area were antagonistic as a result of the intense activity of frugivorous cervids. Interestingly, few seeds spat during rumination by cervids can survive and germinate, resulting in legitimate dispersal (Castañeda et al. 2017), that may be crucial at colonization fronts during natural regeneration processes. However, according to theoretical models the presence or dominance of an interaction typology could create instability in the interactions that structure the plant population (Zarnetske et al. 2012, Mougi and Kondoh 2014). Thus, the dominance of antagonists monopolizing one crucial resource (dwarf palm fruits) could impinge on the interactions and coexistence of the mutualists in the grazed area. Additionally, these theoretical approaches also suggest that the weak interactions with mutualists (dominated by rabbits) that performed only short-distance seed dispersal could destabilize this population.

In the ungrazed area we observed two interaction motifs significantly overrepresented: individual plants that interacted with both mutualists and antagonists and plants without any interaction recorded. As for the first motif, these plants interacted with similar strength with both types of frugivores. In line with the findings by Mougi and Kondoh (2012) and Rodríguez-Rodríguez et al. (2017), this mixture of both interaction types could lead to a more stabilized population than in the grazed area. Future analyses of dwarf palm local demography should test whether a higher presence of complex interactions leading to more diversified plant reproductive outcomes results in increased population stability and ultimately more robust resilience to disturbances. Interestingly, the second motif overrepresented in this area, plants without interactions, is related with the low frugivory effectiveness found in the previous section. Even with a fraction of the palm population showing no interactions with potential dispersers, a mixed frugivore assemblage performing limited-effectiveness dispersal through compensation of the antagonistic effects may result in successful population recruitment.

These results indicate that plants growing in habitats ungrazed received less seed dispersal services compared to those growing in grazed areas. However, the herbivory pressure over the *C. humilis* seedlings, not evaluated here, performed by native and domestic ungulates may influenced the actual low density of dwarf palms in the grazed area (Jácome-Flores et al. 2016). Grazing exclusion in the ungrazed is facilitating the recruitment of *C. humilis*, thus, although the seed dispersal effectiveness is lower in the ungrazed area the probability of seedling survivor is higher than those in the grazed area.

Besides the differences between the degree of protection in each area, we found that the interaction typologies are influenced significantly by plant size and marginally by other traits. Although we detected that antagonistic interactions mostly occurred in large plants that offer ample fruit resources, they dominated along all the range of plant sizes.

On the other hand, mutualistic interactions tended to occur more frequently in small- or medium-sized plants. A possible explanation is that these plants could be less attractive for antagonistic frugivores, leaving fruit resources to other functional groups. If antagonists are only sporadically dependent on dwarf palm fruits, we expect they should select the largest palm patches, leaving isolated and small plants unvisited (Wehncke et al. 2009). Besides, antagonistic frugivores are often considered less efficient in handling and processing fruits (Jordano and Schupp 2000, Simmons et al. 2018), and we expect them seeking higher aggregations of fruit food, such as large clumps of dwarf palms where search and handling costs are minimized.

Effect of interaction motifs on plant seed dispersal effectiveness

Similar to previous findings by Rodríguez-Rodríguez et al. (2017) for plant–pollinator interactions, we found that the best predictor correlated with dwarf palm dispersal effectiveness (a proxy for realized early recruitment) was the predefined interaction typologies. The mixed interaction modes of individual palms with frugivore assemblages combining both mutualists and antagonists had a stronger effect on seed dispersal effectiveness than plant traits or locality. Furthermore, among plants with this interaction typology, those individuals that strongly interact with mutualists had the highest values of effectiveness, and the differences seems to be related to the interaction strength of the antagonistic interactions (Fig. 2). Thus, the overall individual plant SDE is regulated by how strong the plant interacts with the antagonist. Interestingly, although the interaction with antagonists had a significant negative effect on effectiveness, we found that the variation was non-significantly different for plants visited only by mutualists. Two factors can explain this pattern: 1) the proportion of seeds that escape by spitting when antagonists consume the fruits and, 2) the low values of seed dispersal effectiveness of plants visited only by mutualists (Fig. 2). The potential benefits of antagonistic interactions that may marginally result beneficial for plants in combination with the mutualists have been previously reported for pollination mutualisms (Carper et al. 2016, McCall and Irwin 2006, Rodríguez-Rodríguez et al. 2017). In relation to plant–frugivore interactions, marginally efficient antagonists-species that behave as antagonists such as pulp consumers or seed predators yet occasionally contribute legitimate dispersal (Jordano and Schupp 2000, Simmons et al. 2018) may also benefit plants whenever high interaction frequency compensates the detrimental effect of fruit handling damage (Fedriani and Delibes 2013).

Conclusions

Few previous studies have addressed how individual interaction patterns with mutualists and antagonists in plants build up into interaction patterns at larger population- and spatial

scales. The unique dwarf palm illustrates well how interaction frequency alone may not determine interaction outcomes, whenever the variation in fruit handling behaviour or the local food resource supply compensate deficits in any component of seed disperser effectiveness among the frugivorous partners. Our approach helps in understanding how plant–animal interactions occur locally and determine different recruitment scenarios. Furthermore, we showed that the contribution of recruits to the population relies not in the large-size plants but on a few medium-size individuals. This heterogeneity of outcomes at the plant level does not result from many different and highly context-dependent interaction typologies, but from the combination of a few interaction motifs that occur with higher frequency than expected by randomly assembling the pairwise plant–frugivore interactions. We suggest this may be a reasonably frequent situation in diversified frugivore assemblages (Simmons et al. 2018) with a high heterogeneity of functional effects among mutualistic and antagonistic partners.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.8w9ghx3h2> (Jácome-Flores et al. 2019).

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