

Pulp feeders alter plant interactions with subsequent animal associates

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Summary

1. Community context can alter the likelihood of interactions among community members and thus exert critical ecological effects with potential evolutionary implications. For instance, plant–animal mutualisms can be exploited by third species that usurp the resources and/or service that the mutualists offer, while delivering limited or no benefits in return.

2. We experimentally revealed for the first time how exploiters of plant–disperser mutualisms (i.e. pulp feeders) alter the frequency of plant interactions with subsequent mutualistic (seed dispersers) and antagonistic (seed predators) animal associates. In doing so, we chose to study the endozoochore *Pyrus bourgaeana*, which interacts with a diverse assemblage of frugivores including exploiters (pulp-feeding rabbits), legitimate seed dispersers (mammalian carnivores) and seed and fruit predators (rodents and deer, respectively). We hypothesized that pulp feeders would render fruit barely rewarding, affecting subsequent tree–animal interactions.

3. As predicted, pulp removal lessened tree dispersal success (i.e. lowered interaction frequency with seed dispersers) causing an indirect negative effect on its fitness. Furthermore, pulp feeders facilitated foraging by seed-eating rodents, leading to a negative indirect effect on seed survival. Nonetheless, these negative effects of pulp removal on tree fitness were partly counterbalanced by a noticeable decrease in fruit predation by deer. Because both seed dispersers and seed predators preferred large fruits, they exerted selection pressures on fruit size in opposite directions; thus, the net selection regime on fruit size experienced by the tree appeared largely contingent on community composition.

4. Synthesis. Our results illustrate how interactions among functionally distinct frugivores can act synergistically or antagonistically and thus alter their ecological outcomes in ways that differ from those predicted by pairwise interactions. Further research on the relationships between fruiting plants and their consumers will certainly further our understanding of how community context can modify ecological and evolutionary outcomes of complex multispecies interactions.

Key-words: community context, ecosystem services, fleshy-fruited plants, indirect interactions, multispecies interactions, mutualism exploitation, nectar robbers, plant population and community dynamics, pulp thieves, seed dispersal

Introduction

Interactions between plants and their mutualistic animal associates, such as pollination, seed dispersal and defence against herbivores, are pervasive in most ecosystems and paramount for the dynamic and evolution of populations and communities, as well as for the supply of ecological services necessary to human beings (Thompson 2005; Bronstein, Alarcon &

Geber 2006; Agrawal *et al.* 2007; Kremen *et al.* 2007). Such plant–animal mutualisms are often exploited by third species that usurp the resources and/or services the mutualists offer, while delivering limited or no benefits in return (Bronstein 2001). Commendable research efforts on plant–pollination systems (e.g. Morris 1996; Navarro 2000; Genini *et al.* 2010; Irwin *et al.* 2010) have shown that the outcome of mutualism exploitation is often driven through both direct and indirect effects (*sensu* Wootton 1993). Among the direct effects are damage to plant reproductive structures and propagule predation (e.g. Palmer *et al.* 2010). Indirect effects are often

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'trait-mediated', when exploiters change plant traits (e.g. amount of plant rewards) and thus alter the likelihood of subsequent interactions with third species, including other sorts of antagonists and mutualists (Strauss & Irwin 2004; Palmer *et al.* 2010; Whitehead & Poveda 2011). These indirect effects can thus be either positive or negative, depending on whether and how they change subsequent visits by antagonistic or mutualistic animal associates. Therefore, the net effect of mutualism exploitation on plant fitness is difficult to establish and can be negative, neutral or positive (Morris 1996; Navarro 2000; Irwin *et al.* 2010). Nevertheless, we know very little concerning potential direct and indirect effects of exploiters on mutualisms other than plant–pollinator interactions (Irwin *et al.* 2010). In particular, seed–disperser mutualisms play critical roles in many tropical and temperate ecosystems, and thus, disentangling the effects of their exploiters is essential to fully understand the dynamic of plant populations, the assemblage of communities and the resilience of such important ecosystem service (Kremen *et al.* 2007).

Numerous vertebrate-dispersed plants have evolved fleshy fruits that are ingested whole by vertebrates, which transport the seeds internally and disperse them away from the mother plant (i.e. endozoochory). The flesh reward, however, also attracts other fruit consumers that profit from it without ingesting the seeds and, often, without dispersing them (Howe 1977; Wheelwright & Orians 1982; Olesen *et al.* 2010; Fedriani, Zywiec & Delibes 2012; but see Loayza & Knight 2010). These exploiters of plant–disperser mutualisms (or 'pulp thieves'; Howe 1977) can harvest sizeable fractions of tree crops, are widespread and include numerous bird (Snow & Snow 1988; Jordano & Schupp 2000) and mammal species (Howe 1980; Fedriani, Zywiec & Delibes 2012). Surprisingly, even though there has been comprehensive research efforts on fruit–frugivore interactions, whether pulp feeders alter the likelihood of plant subsequent visits by both mutualistic (seed dispersers) and antagonistic (seed predators) animal associates remains a puzzle (e.g. Levey, Silva & Galetti 2002; Dennis *et al.* 2007; Forget *et al.* 2011).

In addition to attracting seed dispersers, the fleshy fruit pulp has other crucial adaptive functions such as acting as physical or chemical defence against seed predators and pathogens (Cipollini & Levey 1997; Tewksbury *et al.* 2008; Fedriani & Delibes 2011). Consequently, by consuming fruit pulp without dispersing the seeds, pulp feeders are expected to lessen the frequency of seed–disperser interactions while enhancing seed predation and pathogen attacks. Importantly, however, pulp feeders could also diminish plant interaction frequency with other frugivores that ingest the whole fruit and destroy all seeds (hereafter 'fruit predators'; Schaefer & Ruxton 2011). Therefore, by reducing the amount of pulp and modifying the fruit traits (i.e. their external aspect), pulp feeders could exert negative and positive effects on plant fitness. Nonetheless, the premise that pulp feeders depress fruit reward and consequently fruit attractiveness in a way that is perceived by subsequent consumers remains untested. The alternative prediction that they do not have an impact on subsequent interactions also needs to be considered because, for

example, in plant–pollinator mutualisms, herbivores and nectar robbers do not necessarily alter plant visitation by legitimate pollinators (see Strauss & Irwin 2004; Irwin *et al.* 2010 reviews).

This study illustrates for the first time how pulp feeders alter fruit attractiveness to subsequent mutualistic and antagonistic plant associates. To this end, we considered the interaction between the endozoochorous *Pyrus bourgaeana* Decne (Rosaceae) and its diverse assemblage of fruit consumers in southern Spain (Fedriani & Delibes 2009a). In addition to pulp feeders (rabbits, small birds), the fruits of this tree are regularly harvested by a variety of vertebrate guilds, including legitimate seed dispersers (mainly carnivores), seed-eating rodents and fruit predators (deer). We hypothesized that pulp feeders would alter the frequency of *P. bourgaeana*'s subsequent interactions with other animal associates and, consequently, the strength of selection pressures on plant traits (e.g. fruit size). Also, since the foraging behaviour and perception abilities of target fruit consumers varied largely (e.g. fruit predators vs. seed-eating rodents), we expected that they would respond differently to fruit defleshing by pulp feeders. To evaluate our hypotheses, we carried out several field experiments where *P. bourgaeana* fleshed and totally or partially defleshed fruits (simulating natural variation in defleshing) of different sizes were offered to mutualistic and antagonistic fruit consumers. We measured the frequency of fruit–frugivore interactions under different treatment combinations and predicted that (i) defleshed fruit would be less attractive to both seed dispersers and fruit predators than intact fruit (Cipollini & Levey 1997), (ii) since defleshed fruits held well-exposed seeds, they would be more likely to be harvested by optimally foraging seed predators (Fedriani & Manzaneda 2005) than whole intact fruits and (iii) because frugivores may respond also to fruit size (Lomáscolo *et al.* 2010), we expected that they would prefer large over small fruits. However, we also predicted that the effect of pulp removal (e.g. a decrease in interaction frequency with frugivores) would be more obvious on large than small fruit, potentially altering the strength of selection pressures on fruit size.

STUDY SYSTEM

The study was carried out during 2011 and 2012 at two *Pyrus bourgaeana* populations in the Doñana National Park (37°9' N, 6°26'W; elevation 0–80 m) in south-western Spain. The climate is Mediterranean subhumid, characterized by dry, hot summers (June–September) and mild, wet winters (November–February). Annual rainfall varies widely, ranging during the last 15 years between 170 and 1030 mm (mean \pm 1SE, 540 \pm 63 mm), with most rain falling during the winter (310.7 \pm 51.4 mm) and extreme drought occurring during the summer (34.1 \pm 7.9 mm; data from 'Natural Processes Monitoring Group', Doñana Biological Station, <http://www-rbd.ebd.csic.es/Seguimiento/mediofisico.htm>). The two target *P. bourgaeana* populations stand on sandy soils and are about 10 km apart from each other. (i) The *Pistacia*-dominated population occurs within a Mediterranean shrubland dominated

by *Pistacia lentiscus* shrubs with sparse understorey of *Chamaerops humilis*, *Halimium halimifolium*, *Stauracanthus genistoides*, *Cistus* spp., etc. Overall local density of fleshy-fruited shrubs in 50 circular plots (1 m diameter) was high (0.50 ± 0.10 shrubs; J. M. Fedriani & M. Delibes, unpubl. data). Local density of *P. bourgaeana* trees is about $0.55 \text{ ind. ha}^{-1}$ (Fedriani & Delibes 2009a). *Quercus suber*, *Olea europaea* var. *sylvestris* and *Fraxinus angustifolia* trees are scattered across the site. (ii) The *Halimium*-dominated population occurs in a shrubland where *H. halimifolium* and *S. genistoides* are the most prevalent shrub species. There are also several fleshy-fruited species such as *Phillyrea angustifolia* and *C. humilis*. Overall local density of fleshy-fruited shrubs in 50 circular plots (1 m diameter) was relatively low (0.26 ± 0.06 shrubs; authors unpublished data). *Q. suber* and patches of *Pinus pinea* trees are scattered across the area. Local density of *P. bourgaeana* trees is about 0.06 ind./ha . Mature individuals of both target populations are frequently aggregated in small clusters (Fedriani, Wiegand & Delibes 2010).

In Doñana, each *P. bourgaeana* individual usually produces yearly between 200 and 450 fruits. After ripening, they drop to the ground from September to December and are harvested by a diverse coterie of frugivores (Fedriani & Delibes 2009a). Fruits are non-dehiscent globose pomes (2–3 cm diameter) weighing ~ 6.7 g, with a sugary water-rich pulp (Fedriani, Zywiec & Delibes 2012). The pericarp comprises three layers, from outer to inner: (i) a green to brownish papery exocarp, (ii) a fleshy well-developed mesocarp and (iii) a cartilaginous endocarp (core) where seeds are tightly implanted. Each fruit contains on average three full seeds. *Pyrus* seeds contain cyanogenic glycosides that are toxic for rabbits and other wildlife (Eisler 1991).

Local seed dispersers of *P. bourgaeana* are mostly medium-sized mammalian carnivores (badger *Meles meles* and red fox *Vulpes vulpes*), though wild boars *Sus scrofa* also disperse some viable seeds (Fedriani & Delibes 2009a). Rabbits and some birds are locally abundant pulp feeders of *P. bourgaeana* fruits. They usually eat to a variable extent the mesocarp (i.e. the pulp) and leave under fruiting trees the uneaten fruit parts with uneaten seeds (Fedriani, Zywiec & Delibes 2012). Seed-eating rodents (mostly *Apodemus sylvaticus* and *Mus spretus*) prey upon seeds mostly from fruits previously defleshed by rabbits (Author, unpublished data). Local fruit predators (deer, *Cervus elaphus* and *Dama dama*) are relatively abundant, ingest whole fallen fruits and grind all ingested seeds (Fedriani & Delibes 2009a; Perea *et al.* 2013).

Materials and methods

FREQUENCY OF FRUIT HARVESTING

To evaluate the combined effect of pulp removal and fruit size on the frequency of fruit harvesting (i.e. consumption of whole fruits, pulp or seeds) by different frugivores, we offered intact and defleshed ripe fruit under fruiting trees at each study site during 2–3 four-day periods in October and November of 2011 and 2012, respectively. We haphazardly chose 25 and 12 fruiting *P. bourgaeana* trees in the *Pistacia*- and

Halimium-dominated study sites, respectively, with >10 m between adjacent trees. Most individual trees (78.4%) were the same in both seasons. Depending on fruit availability, at each experimental tree we set one or two fruit depots. Each depot comprised six ripe fruits collected from each particular tree and offered beneath it. Fruits were set about 10 cm apart from each other within a circular plot (1 m diameter) on a sandy substrate. The field experiments followed a 3×2 randomized complete block design whose factors were ‘pulp removal’ (whole fruits, partially defleshed and almost completely defleshed) and ‘fruit size’ (small and large). Because pulp feeders process *P. bourgaeana* fruits to a variable extent (Fedriani, Zywiec & Delibes 2012), we simulated such variability by offering fruits almost completely defleshed, partially defleshed or whole (i.e. not defleshed or controls). For the partially defleshed treatment, we used a round-tipped knife to remove about a half of the pulp, while carefully avoiding any damage or displacement of the seeds (e.g. Fragoso, Silviu & Correa 2003). For the mostly defleshed treatment, we followed a similar procedure but removed almost all pulp (some tiny pieces of pulp remained attached to the endocarp). Our fruit defleshing treatment left fruits with some seeds partially uncovered and thus visible to predators, resembling the natural conditions after they are harvested by pulp feeders (e.g. rabbits; Fedriani, Zywiec & Delibes 2012). In a sample of 192 fruits from target trees, manual defleshing lead to experimental fruits of $68.2 \pm 0.3\%$ and $33.4 \pm 0.4\%$ of the initial weights for partial and almost complete defleshing treatments, respectively. To select small and large fruits from each tree and for each night, we collected fruits that visually were assessed to represent the extremes of that crop size distribution (i.e. either the largest or smallest fruits). In a sample of experimental fruits ($n = 192$), large-sized fruits (10.8 ± 1.9 g; mean \pm SE) were about 1.9 times heavier than small-sized ones (5.6 ± 1.9 g; $F_{1, 159} = 305.34$, $P < 0.0001$). Fruits infected by invertebrates, aborted, shrivelled or damaged in any way were not used in the field experiments. Though experiments are prone to sustain artificiality, we designed our field experiments based on comprehensive knowledge of the interaction between *P. bourgaeana* and its consumers (e.g. Fedriani & Delibes 2009a,b; Fedriani, Wiegand & Delibes 2010; Fedriani, Zywiec & Delibes 2012). Such deep understanding ensured that our field experiments accurately reassembled natural conditions and pulp defleshing treatments, yielding robust and meaningful results.

Visitors classification was achieved through the identification of their footprints in the local sandy substrate (e.g. Balcomb & Chapman 2003; Mendoza & Dirzo 2007; Fedriani & Delibes 2009a). This approach allowed the differentiation of eight groups of frugivores, which were included into one of the following four frugivore guilds: legitimate seed dispersers (badger, fox and wild boar), pulp feeders (rabbit and birds), fruit predators (deer) and seed-eating rodents (mice and rats). In all experiments, fruits were checked early in the morning during four consecutive days, and the number of harvested fruits under each treatment combination was recorded. Footprints were cleaned at the start of each field experiment and again after each observation. Fruits belonging to all treatment combinations were replaced with fresh ones each morning.

STATISTICAL ANALYSES

The results were analysed by fitting generalized linear mixed models using the Proc Glimmix from SAS (Little *et al.* 2006), which allows the modelling of non-normal response variables as well as the usage of both fixed and random factors. We modelled the conditional likelihood of fruit harvesting (given that a tree was visited by a particular frugivore guild) as a function of frugivore guild, fruit size and pulp

removal (factor levels as described above) considering only trees visited by a single frugivore guild during a particular night. Also, we included in this model all second- and third-order interactions between main factors. Season (2011 or 2012), sampling date (nested within season), locality (two populations), experimental tree (nested within locality) and fruit depot (nested within tree and population) were included as random factors. Because of the binomial nature of the response variable (fruit harvest [1/0]), binomial error and logit link function were specified. When the interaction between any two factors was significant, tests for the effect of a given factor at the different levels of the other factor (i.e. tests of slices) were performed using the SLICE option in the LSMEANS statement of the MIXED procedure (Little *et al.* 2006).

Results

TREE VISITATION AND FRUIT HARVESTING

Frugivore tracks and/or other signs such as faeces or rooting were found by the fruit in all experimental *P. bourgaeana* trees and on most trials (87.2%; $n = 507$ night-trees). During the 442 recorded frugivore visits to target trees (minimum estimate, since occasionally more than one individual could be involved in a single visit), each visitation was undertaken by 1.20 ± 0.022 (mean \pm 1SE) different consumers (range, 1–3). The frequency of visits by different guilds varied between study sites ($\chi^2 = 137.1$, d.f. = 3, $P < 0.0001$). Whereas pulp feeders were more frequent in the *Pistacia*-dominated (49.5%) than in the *Halimium*-dominated shrubland (11.4%), fruit predators were more frequent in the last (67.3%) than in the former one (17.8%). For legitimate dispersers and seed-eating rodents, however, the frequencies of visits were more alike in the *Pistacia*- and *Halimium*-dominated shrublands (26.1 vs. 18.2% and 13.6 vs. 10.4%, respectively). Overall, 78.0% of visits belonged to single visitors. Of them, 40.8% were fruit predators (deer), 20.9% pulp feeders (rabbit and small birds), 9.8% legitimate seed dispersers (carnivores and wild boar) and 6.5% seed-eating rodents.

Most frugivore visits (82.2%, $n = 442$) resulted in fruit harvesting and, on average, about five (4.8 ± 0.1) of the six offered fruits were harvested each time. Our mixed model for single visitor data revealed that, once controlled for the effects of random factors, guilds differed in fruit-harvesting likelihood ($P = 0.010$; Table 1a). Specifically, once a *P. bourgaeana* tree was visited by a particular frugivore guild, the probability of fruit harvesting was highest for fruit predators (0.916 ± 0.096), lowest for seed dispersers (0.739 ± 0.249) and intermediate for seed-eating rodent (0.857 ± 0.159) and pulp thieves (0.796 ± 0.203).

EFFECT OF PULP REMOVAL AND FRUIT SIZE ON HARVESTING LIKELIHOOD

As a whole, frugivores significantly preferred large over small fruits ($P = 0.046$; Table 1a). Moreover, the non-significant second-order interaction between fruit size and frugivore guild ($P = 0.558$) indicated that the trend was consistent across

Table 1. (a) Results of main effect tests using generalized linear mixed models on the effects of pulp removal (P), fruit size (S), consumer guild (G) and their second- and third-order interactions, on the conditional likelihood of harvesting *Pyrus bourgaeana* fruit. (b) Since there were two significant second-order interactions, we performed tests for the effect of a given factor at the different levels of the other factor (i.e. test of slices). Though only fixed effects are shown, our mixed model also corrected for the effect of random effects [i.e. season, sampling date (nested within season), locality, experimental tree (nested within locality) and fruit depot (nested within tree and population)]. Significant values ($P < 0.05$) are shown in bold

	d.f.	F	P
(a) Tests of main effects			
Pulp removal (P)	2, 1576	9.20	<0.0001
Size (S)	1, 1576	4.00	0.046
Guild (G)	3, 1576	3.77	0.010
S*P	2, 1576	4.23	0.015
P*G	6, 1576	4.81	<0.0001
S*G	3, 1576	0.69	0.558
P*S*G	6, 1576	1.13	0.340
(b) Tests of slices			
Interaction S*P			
Large fruits	3, 1576	4.02	0.007
Small fruits	3, 1576	1.73	0.159
Interaction P*G			
Fruit predators	2, 1576	16.82	<0.0001
Seed dispersers	2, 1576	6.11	0.002
Seed-eating rodents	2, 1576	2.66	0.069
Pulp thieves	2, 1576	3.99	0.019

guilds (Fig. 1a). Nonetheless, tests of differences between least square means for each single guild indicated that preference on large fruits was only significant for fruit predators (Fig. 1a). The significant interaction between fruit size and pulp removal indicated that, as predicted, whereas pulp removal significantly (test of slices, $P < 0.007$; Table 1b) decreased the overall likelihood of harvesting large fruit, pulp removal did not have a significant effect on small fruit harvesting (test of slices, $P = 0.226$; Figs 1a and 2a).

The overall probability of fruit harvesting significantly decreased with pulp removal ($P < 0.0001$; Table 1a). Whole fruits and partially defleshed fruits showed harvesting probabilities on average 1.3-fold higher than defleshed fruits. Interestingly, however, the interaction between pulp removal and consumer guild was strongly significant ($P < 0.0001$, Table 1a); as predicted, the sign of pulp removal effect on fruit harvesting was not consistent across consumer guilds (Figs 1b, 2b). In particular, seed dispersers, pulp feeders and fruit predators showed likelihoods of harvesting whole fruits 2.7-, 1.3- and 1.2-fold higher than those for defleshed fruits. Conversely, seed-eating rodents showed a likelihood of harvesting defleshed fruits 1.2-fold higher than that for whole ripe fruits (Fig. 2b). These differences between guilds in harvesting likelihood were significant for the three pulp removal levels (tests of slices, $P < 0.050$; Table 1b). Other second- and third-order interactions were not significant (Table 1a).

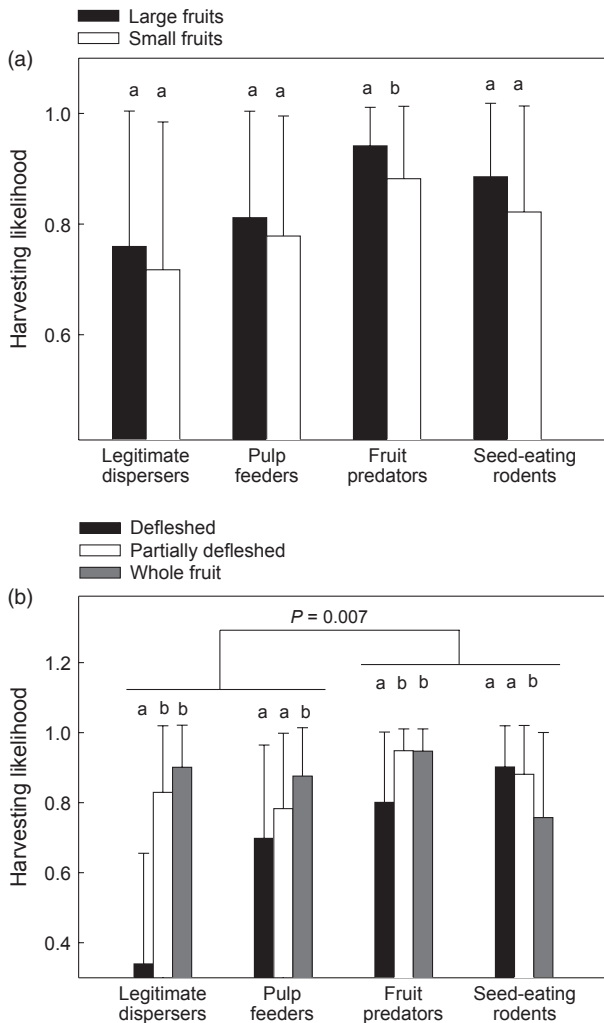


Fig. 1. Model-corrected mean percentages (\pm ISE) of *Pyrus bourgaeana* fruit harvest likelihood by different consumer guilds as a function of (A) pericarp removal and (B) fruit size during field experiments in two consecutive years at two localities of south-western Spain. For each guild, different lowercase letters among pericarp treatments denote significant ($P < 0.05$) differences.

Discussion

By simulating the modification of fruit traits exerted by pulp feeders, our study provides novel experimental evidence of how trait-mediated effects alter the strength of subsequent plant interactions with both mutualistic and antagonistic consumers of fruit and seed. Importantly, unlike in most nectar- and pollen-rewarding flowers, fruit rewards (pulp, arils) are often visible to consumers from a distance and thus potentially accounted for in foraging decision-making (Schaefer & Ruxton 2011). Nonetheless, because the foraging behaviour and perception abilities (e.g. sight, smell) of contrasting guild consumers vary largely (Schaefer & Ruxton 2011), examining how pulp feeders alter fruit attractiveness to subsequent mutualistic and antagonistic plant associates is a noticeable pending task required to unravel the complexity of such multispecific interactions (see Rodríguez, Alquézar & Peña

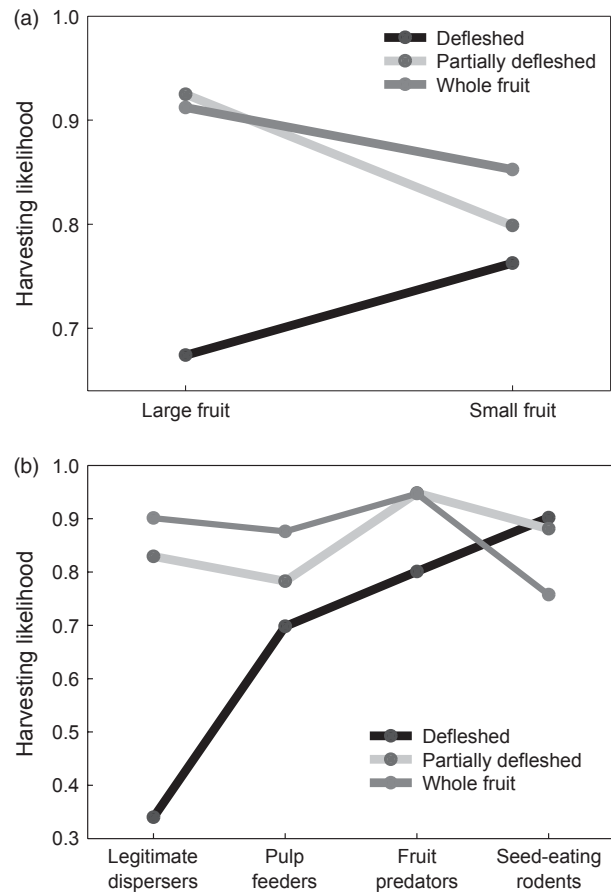


Fig. 2. Graphical representation of statistically significant interactions found for our field experiments with *Pyrus bourgaeana* fruit. (A) Interaction between pulp removal and fruit size showing how the effect of defleshing on harvesting likelihood was much higher for large than for small fruit. (B) Interaction between pulp removal and frugivore guild. The negative effect of fruit defleshing on harvesting likelihood was especially marked for legitimate dispersers. Also, note that fruit defleshing had a positive effect on seed-eating rodent harvesting likelihood.

2013 review). Moreover, fruit–frugivore interactions are key processes in most tropical and temperate ecosystems (Dennis *et al.* 2007), and disentangling their complex interactions is necessary to fully understand the dynamics of populations, communities and essential ecosystem services (Kremen *et al.* 2007).

As predicted, our results revealed that pulp feeders can alter the interaction frequency between fleshy-fruited plants and their mutualistic and antagonistic animal associates. In the case of *P. bourgaeana*, such changes can have variable effects on plant-dispersal success, as sketched in Fig. 3. First, by lessening the interaction frequency with legitimate dispersers (e.g. badgers, foxes; Fedriani & Delibes 2009a,b), pulp feeders probably reduce *P. bourgaeana*'s long-distance dispersal and colonization ability (Levin *et al.* 2003; Nathan *et al.* 2008), causing a trait-mediated negative effect on tree fitness. Secondly, pulp feeders enhanced the foraging by seed-eating rodents, thus leading to an additional negative indirect effect on seed survival (Fig. 3). Nonetheless, these

negative effects of exploitation by pulp feeders would appear counterbalanced, at least partially, by some positive effects. Specifically, pulp removal decreased the interaction frequency with the abundant ungulate fruit predators yielding thus an indirect positive effect on seed survival (Fig. 3). Moreover, the benefits of pulp feeders also concern critical plant stages other than seed dispersal. In particular, Fedriani, Zywiec & Delibes (2012) recently have proved that pulp feeders can exert sizeable direct positive effects on *P. bourgaeana* seedling emergence, survival and establishment (Fig. 3). Therefore, target tree and functionally diverse animal associates appear to shape a complex web of direct and indirect effects often acting in opposite directions, whose net effect is probably dependent on the community context (Bronstein 1994; Strauss & Irwin 2004; Agrawal *et al.* 2007).

Recent consumer–resource models on the dynamic of exploited mutualisms predict that their outcome is strongly dependent on initial population densities (Wang, DeAngelis & Holland 2012). In the case of exploited seed–disperser mutualisms, the net effect of pulp feeders on seed fate probably will result from, among other factors, the abundance of legitimate dispersers, fruit and seed predators. In our studied multi-specific system, rodent abundance show dramatic interannual changes (Kufner 1986; authors unpublished data); thus, the

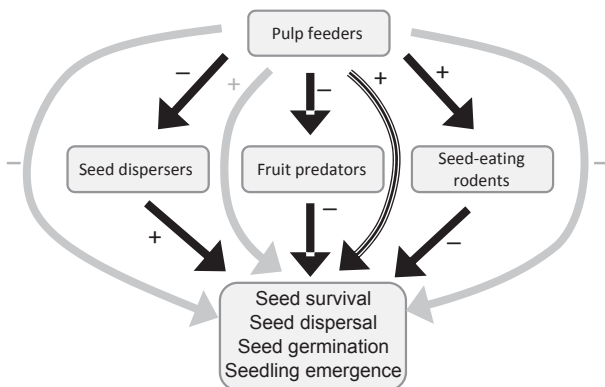


Fig. 3. Sketch of the myriad pathways and mechanisms leading to potential effects of pulp feeders on seed survival and dispersal. Plus and minus symbols signify whether the outcome of interactions (represented by arrows) is beneficial or detrimental for plant fitness. Whereas pulp removal by pulp feeders (rabbits, birds) directly decreases endozoochore interaction frequency with both legitimate seed dispersers (carnivores, wild boar) and fruit predators (deer; black arrows), it enhances foraging by seed-eating rodents (black arrows). As a consequence of such direct effects, there are three indirect trait-mediated effects exerted by pulp feeders (grey arrows) on plant fitness: (i) because seed dispersers exert direct positive effects on seed dispersal (black arrow), pulp feeders have an indirect negative effect on dispersal success (grey arrow), (ii) given that seed-eating rodents exert direct negative effects on seed survival (black arrow), pulp feeders have an indirect negative effect on dispersal success (grey arrow) and (iii) since fruit predators exert direct negative effects on seed survival (black arrow), pulp feeders have an indirect positive effect on seed survival (grey arrow). Pulp feeders can also benefit fruiting plants during ontogenic stages other than seed survival and dispersal. Fedriani, Zywiec & Delibes (2012) recently have proved that pulp feeders can exert sizeable direct positive effects on seedling emergence, survival and establishment, which are represented by a triple-lined black arrow.

net effect of pulp feeders on plant recruitment could shift from negative, when rodents are abundant enough to prey upon most defleshed *P. bourgaeana* seeds, to positive during the years of low rodent abundance. On the other hand, since pulp feeders often lessen long-distance dispersal (Fig. 3) while enhancing local recruitment (Fedriani, Zywiec & Delibes 2012), we would expect that, for fixed abundances of the remaining frugivores, pulp feeders would have a net negative effect on plant fitness when suitable habitat and seed dispersers are fully available. Conversely, pulp feeders might provide a net positive effect on plant fitness under scenarios of severe scarcity of suitable habitats and/or legitimate dispersers, as frequently occurs due to human activity (Bonte *et al.* 2012; Galetti *et al.* 2013). Interplay between theory and empirical research is needed to unravel the conditional dynamic (*sensu* Bronstein 1994) of these complex multispecific interactions and the circumstances under which they can persist (Ferrière *et al.* 2002; Holland & DeAngelis 2010; Wang, DeAngelis & Holland 2012).

Mutualistic and antagonistic animal associates can exert selection pressures on plant traits in the same or in opposite directions (Herrera 2009; Irwin *et al.* 2010). Our results showed that preference of different fruit sizes by frugivores was weak, especially when considering each guild separately. Furthermore, even assuming weak preference for larger fruits by all fruit consumers (Fig. 1a), seed dispersers and seed/fruit predators would exert opposed selection pressures on fruit size, thus, probably counteracting each other. Conflicting selection pressures on fruit traits by mutualistic and antagonistic interactors have been documented in other fleshy-fruited (Alcántara & Rey 2003; Martínez, García & Obeso 2006) and conifer species (Siepielski & Benkman 2007). Given the likely temporal and spatial inconsistencies in the abundance of different plant associates (Thompson 2005) and recent evidence of rapid microevolutionary change in fruit traits following selective defaunation (Galetti *et al.* 2013), further investigations are certainly needed to make inferences concerning the potential selection pressures of pulp feeders on endozoochores.

Lack of research about pulp feeder effects on endozoochore successive interactions contrasts with the well-documented effects of exploiters of plant–pollinator mutualisms (Irwin *et al.* 2010; but see Traveset, Willson & Gaither 1995; García *et al.* 1999). Such shortage of studies is even more surprising given the intensive and prolific research on fruit–frugivore interactions (e.g. Levey, Silva & Galetti 2002; Dennis *et al.* 2007; Forget *et al.* 2011). Nonetheless, scattered through the literature are several reported cases concerning birds, rodents, primates and pigs consuming the rewards without dispersing the seeds of diverse endozoochores, including Rosaceae, Moraceae, Burseraceae, Rubiaceae, Arecaceae in tropical, neotropical and temperate ecosystems all over the world (Lombardero 2012). For example, in the Mediterranean Europe, nine species of small birds acting as pulp feeders comprised up to 35% and 25% of total frugivore visits and fruit removal, respectively, of fruiting *Prunus mahaleb* trees (Jordano & Schupp 2000). Given such lack of research and

the fact that fleshy-fruited plants are keystone species in most tropical and temperate forest (Dennis *et al.* 2007), synthesizing investigations on the pervasiveness and ecological correlates of these overlooked multispecies interactions are desirable.

To conclude, we revealed that pulp feeders can exert previously unnoticed positive and negative trait-mediated effects on endozoochores and suggest that pulp thieving may be an integral part of endozoochore–seed disperser mutualisms. The types of higher order interactions that result from the action of pulp feeders, seed dispersers and seed/fruit predators may damp, or reverse, any selective effect of pairwise interactions on plant traits related to seed dispersal. Our study exemplifies how fruiting plants and their consumers are valuable systems to further our understanding of how community context can alter ecological and evolutionary outcomes of multispecies interactions, opening up a new avenue of research.

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