The overlooked benefits of synzoochory: rodents rescue seeds from aborted fruits

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Abstract.   Large-scale abortion of immature fruits is a pervasive phenomenon across seed plants due to maternal physiological decisions associated with matching resources with fruit crop size. Aborted fruits are usually disqualified from studies of both fruit production and seed dispersal. However, a considerable number of developing seeds occur within immature aborted fruits. We evaluated the untested hypotheses that seeds within aborted fruits are viable and that incomplete predation of seeds within aborted fruits by hoarding rodents provides, in addition to seed movement, increased germination and seedling emergence. To this end, we studied the system composed by the Iberian pear *Pyrus bourgaeana* and several rodent species in Mediterranean Spain. About a third of aborted fruits found beneath tree canopies (n = 2430) were partially eaten by rodents. Using a seed sowing experiment, we revealed that a considerable fraction of seeds from *P. bourgaeana* aborted fruits are viable, germinating, and emerging seedlings. Paradoxically, however, these seeds are de facto unviable since they are confined within the extremely hard pericarp of aborted fruits, which prevents any seedling emergence and thus any contribution to tree recruitment. We show that only when rodents partially gnaw the pericarp walls of aborted fruits, seeds that escaped from predation have the prospect of emerging and thus potentially contributing to tree regeneration. Thus, in this and probably in many other similar synzoochore systems, rodents act as rescuers of seeds confined within aborted fruits, conferring the plants a largely overlooked benefit that could shape the reproductive strategy of many plant species.

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INTRODUCTION

Despite the fact that ecological interactions are often described as either antagonistic or mutualistic, most of them correspond to a mixture of conflicting and overlapping interests, with the capacity of being positive or negative for the participants (Bronstein 2001, Van Baalen and Jansen 2001, Fedriani and Delibes 2011, Kiers et al.

2011). The costs and benefits characterizing most species interactions are neither necessarily obvious nor fixed, and often change along the ontogeny of interacting species as well as in space and time (Bronstein 1994, Fedriani et al. 2012, Chamberlain et al. 2014). Identifying these costs and benefits is essential to comprehensively understand the position of species interactions

within the mutualism–antagonism continuum and thus their potential ecological and evolutionary outcomes (Perea et al. 2013, Bronstein 2015, Gómez et al. 2019).

Seed dispersal is a very versatile demographic process with critical consequences for plant dynamics and the assemblage of entire communities (van der Pijl 1982, Herrera and Pellmyr 2002, Schupp et al. 2010). Seed dispersal by animals is achieved through varied mechanisms. Seeds can be transported on the outside of (epizoochory) or inside (endozoochory) animals that eventually deliver the seeds away from the often hazardous maternal environment (Herrera 2002). Also, some seed-eating animals transport seeds in the mouth or inside their cheeks followed by the hoarding of at least a fraction of those seeds (synzoochory; see Gómez et al. 2019 review). In these synzoochorous systems, seeds that are not consumed immediately may benefit from being stored some distance away from the mother plant and forgotten, enhancing seed survival and thus the population persistence as well as the chances of colonization of vacant habitats (Vander Wall 1990, Iluz 2011). Thus, in synzochore systems the animal partner plays a dual role, acting both as seed disperser and seed predator.

Most research on synzoochory has focused on seed movement-related benefits (Vander Wall 2002, Zwolak et al. 2016, Gómez et al. 2019). Nonetheless, some authors reported that in some large-seeded species (e.g., *Quercus* spp.) partial seed consumption by rodents and other consumers may not harm, or may even increase, their prospects of establishment (Steele et al. 2007, Perez et al. 2008, Perea et al. 2011, Loayza et al. 2014). Besides, Peterson and Parker (2016) suggested that seed caching and burial by rodents increased seed survival during fire events. Interestingly, there exist other potential though overlooked benefits of synzoochory for plant species producing multi-seeded fruits. Namely, multi-seeded fruits are often partially gnawed by rodents and the breaking of the fruit pericarp facilitates seed germination and seedling emergence (e.g., Peres and Baider 1997, Fedriani et al. 2012) of any seeds that escape from predation (Bollen et al. 2004). These potential benefits seem most relevant for plant species producing multi-seeded fruits with hard pericarps that strikingly hamper seedling emergence

(e.g., many nuts, figs, and citrus; Bradford and Smith 1977, Baskin and Baskin 2014). Surprisingly, we are not aware of any investigation addressing whether and how partial consumption of multi-seeded fruits by seed predators facilitates seed germination and seedling emergence of surviving seeds.

Large-scale fruit abortion of immature fruits is a pervasive phenomenon across seed plants; it is due to either damage to the fruit or seed, or to maternal physiological decisions associated with matching resources with fruit crop size or with optimizing genetic composition of the crop (Lloyd 1980, Janzen 1983, Aizen and Harder 2007). Aborted fruits are not usually considered in studies of neither fruit production nor seed dispersal since the number of viable seeds within them is often assumed to be zero (e.g., Khan et al. 1999, Young et al., 2007, Fedriani et al. 2015). However, a large though variable number of developing seeds may occur within immature fruits (e.g., Bawa and Webb 1984). Whether aborted fruits that have fallen down early in their development contain potentially viable seeds, and whether those seeds are dispersed (e.g., by synzoochory) and thus could contribute to natural regeneration, has not been examined yet.

We evaluate the untested hypotheses that seeds within aborted fruits are viable and that partial consumption of aborted fruits by hoarding rodents provides, in addition to seed movement, increased germination and seedling emergence. To this end, we studied the system composed by the Iberian pear *Pyrus bourgaeana* and several rodent species in Mediterranean Spain. This tree aborts a large fraction of its crop by early abscission of immature fruits well before fruit ripening in autumn (Fedriani et al. 2015). Intriguingly, rodents of several species frequently hoard aborted fruits and eventually consume most (but not all) of their seeds (authors of this study, *unpublished data*). Because of the hard pericarp of *P. bourgaeana* aborted fruits, we predicted that, in case they contain any viable seeds, partial consumption by rodents (i.e., pericarp fracture) would increase seed germination and seedling emergence. However, the potential of seeds contained within *P. bourgaeana* aborted fruits to recruit is unknown. Here, we first evaluated potential differences in key traits (fruit and seed size, seed number, and insect seed predation)

between *P. bourgaeana* aborted and ripe fruits. Then, we conducted an experimental sowing using seeds from aborted and ripe fruits and addressed the following three specific questions: (1) Do aborted fruits contain viable seeds? (2) If so, is the pericarp breakage by rodents a requisite for seed germination and seedling emergence from aborted fruits? and (3) Does the probability of seed germination and seedling emergence differ between seeds from aborted and ripe fruits?

Methods

Study site and species

Pyrus bourgaeana is a deciduous small tree endemic to the Iberian Peninsula and North Africa (Aldasoro et al. 1996). The study was conducted during the fall and the winter of 2011, in the Doñana National Park (37°9′ N, 6°26′ W; elevation 0–80 m; Fig. 1) in southwestern Spain. The climate is Mediterranean sub-humid, with dry and hot summers (June–September), and mild, wet winters (November–March; Żywiec et al. 2012). The distribution of *P. bourgaeana* in Doñana is highly fragmented, with trees occupying patches of Mediterranean scrubland at low densities (usually < 1 individual/ha), with occupied patches isolated from each other by natural and human barriers (Fedriani et al. 2010). We chose one of these Mediterranean scrubland patches (called Matasgordas; ~310 ha; Fig. 1) vegetated mainly by *Pistacia lentiscus* shrubs with variable cover of *Halimium halimifolium*, *Stauracanthus genistoides*, and *Chamaerops humilis* shrubs and with scattered *P. bourgaeana*, *Quercus suber*, *Fraxinus angustifolia*, and *Olea europaea* var. *sylvestris* trees.

In Doñana, the reproduction and regeneration of this tree is very limited due to factors such as high mortality of seeds and seedlings, and seed dispersal limitation (Fedriani et al. 2019, 2020). As a consequence, the population shows a marked left-skewed demographic structure, with many individuals of older age classes, few juveniles, and even fewer seedlings and saplings (Żywiec et al. 2017). *Pyrus bourgaeana* aborts a large fraction of its crop by early abscission of immature fruits during May–August, well before the usual ripening season (September–November; Fedriani et al. 2015). Fruit abortion and dropping are thought to be induced by poor pollination quality, frosts, and invertebrate attacks (Fedriani et al. 2015). These aborted fruits are of small size (1–2 cm), dark brown, and dry, and each one includes usually 0–3 apparently developed seeds (25–50 mg each; authors of this study, *unpublished data*; Fig. 2) within very hard pericarps. The potential of seeds from aborted fruits to germinate and contribute to recruitment has been assumed to be nil (Fedriani et al. 2015, Castilla et al. 2019). Fruits that complete their development are globose, fleshy pomes, and noticeably larger (~9.5 g and 2–4 cm in diameter; Fedriani et al. 2012, Garrote et al. 2018) than the aborted ones. Each fruit includes 1–5 viable seeds (46–91 mg each; Fedriani and Delibes 2009). Seeds within ripe fruits are mostly dispersed by frugivorous red foxes (*Vulpes vulpes*) and badgers (*Meles meles*; Fedriani et al. 2018, 2020), but these dispersers do not ingest aborted dry fruits. The seeds produced in both aborted and ripe fruits are dark brown and have a pyriform shape. Pre-dispersal *P. bourgaeana* seed losses due to insects (microlepidoptera larvae) are thought to be low (Fedriani and Delibes 2009).

Several species of generalist rodents (e.g., *Apodemus sylvaticus*, *Mus spretus*, *Rattus* spp., and *Eliomys quercinus*) are known to feed on dispersed seeds from ripe fleshy fruits (Suárez-Esteban et al., 2018, Garrote et al. 2018). Rodents often gnaw *P. bourgaeana* aborted fruits along their longitudinal axis taking all or, most often, some of their seeds; thus, rodents recurrently leave some partially gnawed fruits with uneaten seeds (Fig. 2; authors of this study, *unpublished data*). Indeed, small clusters of intact (i.e., ungnawed by rodents) and partially gnawed aborted fruits containing seeds escaped from predation (~4–8 fruits per cluster) are often found beneath fruiting trees and also within nearby *P. lentiscus* shrubs (authors of this study, *personal observations*). These aborted fruits do not break open upon fruit fall, and thus, their seeds are doomed to remain trapped inside their hard pericarps, unless the fruits are gnawed open or fractured by vertebrate seed predators (e.g., Peres and Baider 1997).

Fruit sampling and characterization

To quantify the extent to which *P. bourgaeana* aborted and ripe fruits differ and to assess whether aborted fruits contain (apparently) developed seeds, we characterized the traits of both
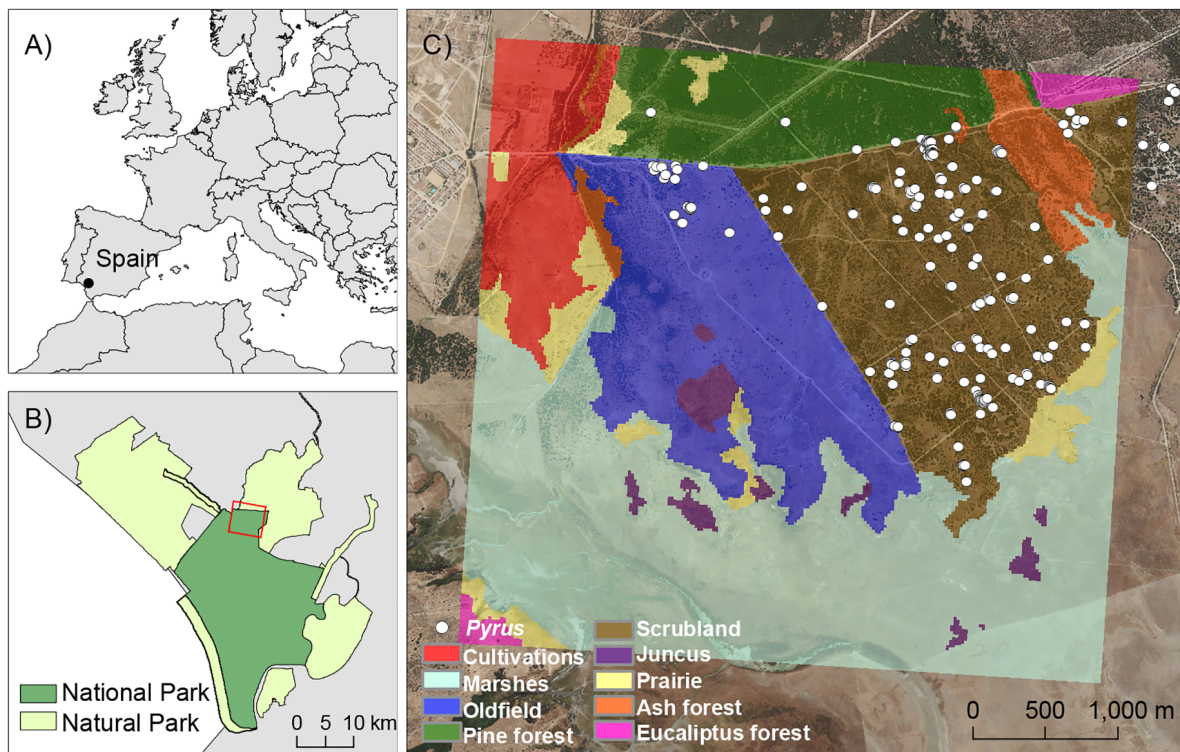
Fig. 1. Location of the Doñana National Park (DNP) in southwestern Spain (A), location of our study site (Matasgordas) within the DNP (B), and detailed view of Matasgordas and its main habitat types (C). The white disks represent the reproductive *Pyrus bourgaeanea* trees.

types of fruits collected from 64 fruiting trees in early September 2011 (fallen aborted fruits) and early November 2011 (ripe fruits). For most trees (81.3%), both fruit types were sampled. Overall, we characterized 188 ripe, 445 partially gnawed aborted, and 746 intact aborted fruits, which contained 457, 290, and 931 developed seeds, respectively. Seeds from ripe fleshy fruits were easily extracted using a jack-knife, whereas dry aborted fruits were hard and difficult to crack and thus pliers were needed. The relative low number of seeds within partially gnawed aborted fruits was likely the result of seed removal by rodents before fruits were sampled. Because many seeds within both aborted and ripe fruits were attacked by insects, we also evaluated whether insect seed predation varied among fruit types. Fruits of shriveled aspect were not considered.

The seed germination experiment

To evaluate whether and how many *P. bourgaeana* seeds within aborted fruits could contribute to tree recruitment, we used the seed samples mentioned above plus additional ones to set up a germination experiment in November 2011. We considered the following four seed treatments: (1) clean seeds from ripe fruits ($n = 199$); (2) clean seeds from intact aborted fruits ($n = 994$); (3) seeds within partially gnawed aborted fruits ($n = 643$); and (4) seeds within intact aborted fruits ($n = 498$). Seeds and aborted fruits were sown 2–3 mm deep in separate pots (8 × 8 × 18 cm), and the pots were placed in a common garden under the natural regime of precipitation (i.e., no additional watering). For intact and partially gnawed aborted fruits, we placed 3.67 ± 0.13 fruits per pot (range 1–5). For clean seeds from ripe or aborted fruits, we placed 6.83 ± 0.37 seeds per depot (range 1–12). Date of emergence was recorded every other week till April 2012. Emergence was defined as the protrusion of cotyledons above the soil surface. To estimate seed germination (and also to estimate the number of seeds included within intact and partially

Fig. 2. Aborted and ripe *Pyrus bourgaeana* fruits still attached (A) and fallen underneath a reproductive tree (B).

gnawed aborted fruits), we retrieved experimental seeds (or remains) from all pots ($n = 309$) at the end of the study. Germination takes place from the proximal base of the seed, with the testa splitting along its longitudinal axis into halves. Numerous split testas in pots with no emerged seedlings were often found, indicating failure between germination and emergence. Considering all four seed treatments, we retrieved remains of 2334 seeds, which were categorized as germinated, dried out, or predated by insects (e.g., Fedriani et al. 2012). Because most of these insect seed predation events likely occurred before the experiment was set up, predated seeds were excluded from the calculations to estimate percentages of seed germination.

Statistical analyses

We evaluated trait (fruit and seed size, number of seeds, and proportional insect seed predation)

differences between aborted and ripe fruit by fitting generalized linear mixed models using Proc Glimmix (SAS Institute 2018). For these three response variables, we specified in the models the appropriate error (Normal, Poisson, and Binomial, respectively) and the canonical link functions (SAS Institute 2018). Fruit type was specified in the models as fixed effect, whereas individual tree was included as random factor. To compare the effects of different levels of any significant factor, we calculated the differences between their least square means.

To evaluate the effect of seed treatment (e.g., clean seeds *vs*. seeds within aborted fruits) on germination, we fitted a generalized linear mixed model with Binomial error and logit link function. Seed treatment was specified in the model as fixed effect, whereas individual tree was included as random factor (other conventions are as described above). Due to low number of emerged seedlings (55 in overall), we evaluated differences among seed treatments by chi-squared analyses of contingency tables using Proc Freq in SAS (SAS Institute 2018).

RESULTS

Fruit and seed traits

Most *P. bourgaeana* trees within our study plot accumulated large numbers of intact and partially gnawed aborted fruits beneath their canopies. Specifically, we rigorously sampled four trees that had underneath 607.5 ± 148.1 (mean $\pm$ 1 SE) aborted fruits, with about a third of them ($31.6\% \pm 5.4$; $n = 2430$) being partially eaten by rodents. These same trees produced on average 958.0 ± 323.6 ripe fruits; thus, about 38.8% of total produced fruits ($n = 3852$) by these trees were aborted ones.

Measured *P. bourgaeana* fruit traits generally differed between aborted and ripe fruits (Fig. 2). Ripe fruits were on average about three times heavier (5.33 ± 0.15) than aborted fruits (1.53 ± 0.14; $F_{1,66} = 721.2$, $P < 0.0001$). There were overall significant differences in the number of apparently developed seeds contained across the three types of fruits considered (ripe, intact aborted, and partially gnawed aborted; $F_{2,174} = 44.09$, $P < 0.0001$; Fig. 3A). Ripe and intact aborted fruits had on average similar number of apparently developed seeds (differences in

least square means, $t = 1.27$, $P = 0.206$), which was about two times higher than that of partially gnawed aborted fruits ($t = 8.39$, $P < 0.0001$; Fig. 3A). Seeds from ripe fruits were on average 2.5 times heavier than those from intact and partially gnawed aborted fruits ($F_{2,624} = 388.53$, $P < 0.0001$; Fig. 3B). Seeds from intact aborted fruits were only slightly but significantly (1.1 times) heavier than those of partially gnawed aborted fruits ($t = 2.43$, $P < 0.05$; Fig. 3B). The percentage of insect seed predation varied among fruit types ($F_{2,508} = 4.09$, $P < 0.05$; Fig. 3C), with partially gnawed aborted fruits showing higher seed predation than both ripe and intact aborted fruits ($t > 2.37$, $P < 0.05$).

Seed germination and seedling emergence

In our sowing experiment, we found strong overall differences among the four *P. bourgaeana* seed treatments on percentage of seed germination ($F_{3,\ 216} = 46.62$, $P < 0.0001$; Fig. 4). Specifically, percentage of germination of clean seeds from ripe fruits was 3.4, 4.7, and 30.8 times higher than that of clean seeds from aborted fruits, seeds within partially gnawed aborted fruits, and seeds within intact aborted fruits, respectively ($t > 7.45$, $P < 0.0001$). Furthermore, clean seeds from aborted fruits and seeds within partially gnawed aborted fruits showed 6.5 and 9.1 times higher germination percentages than seeds within intact aborted fruits, respectively ($t > 5.44$, $P < 0.0001$; Fig. 4). Except for seeds within intact aborted fruits ($n = 401$), all other seed treatments led to emerged seedlings. Specifically, 7.1% ($n = 842$), 7.1% ($n = 437$) and 4.3% ($n = 93$) of clean seeds from aborted fruits, seeds within partially gnawed aborted fruits, and clean seeds from ripe fruits emerged seedlings, respectively. These differences among seed treatments on emergence rates were significant when all four treatments were considered (chi-squared test, $\chi^2 = 34.34$, df = 3, $P < 0.0001$) and turned marginally significant when seeds within intact aborted fruits were excluded from the analysis ($\chi^2 = 5.34$, df = 2, $P = 0.069$).

DISCUSSION

Studies of fruit and seed development typically consider only two possible fates, abortion, or complete development. The possibility that
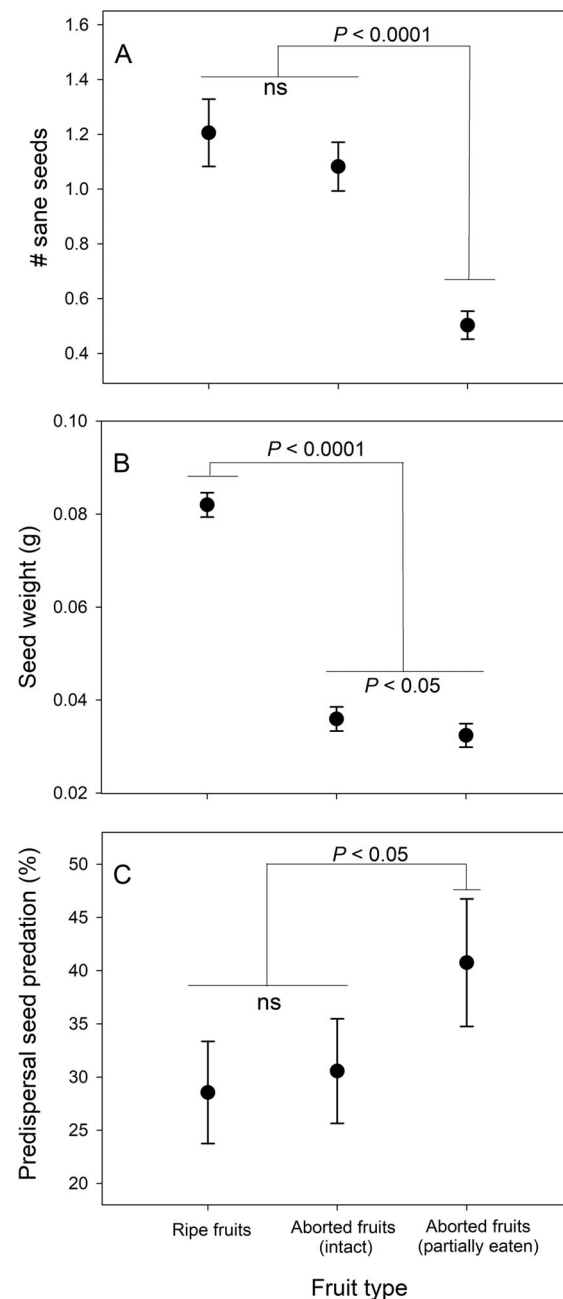

Fig. 3. Model-adjusted mean ($\pm$ 1 SE) numbers of *Pyrus bourgaeana* seeds per fruit (A), seed weight (B), and percentage of insect seed predation (C) for ripe, intact aborted, and partially eaten aborted fruits.

seeds from aborted fruits that fall down early in the development have the potential to contribute to natural regeneration has been ruled out time
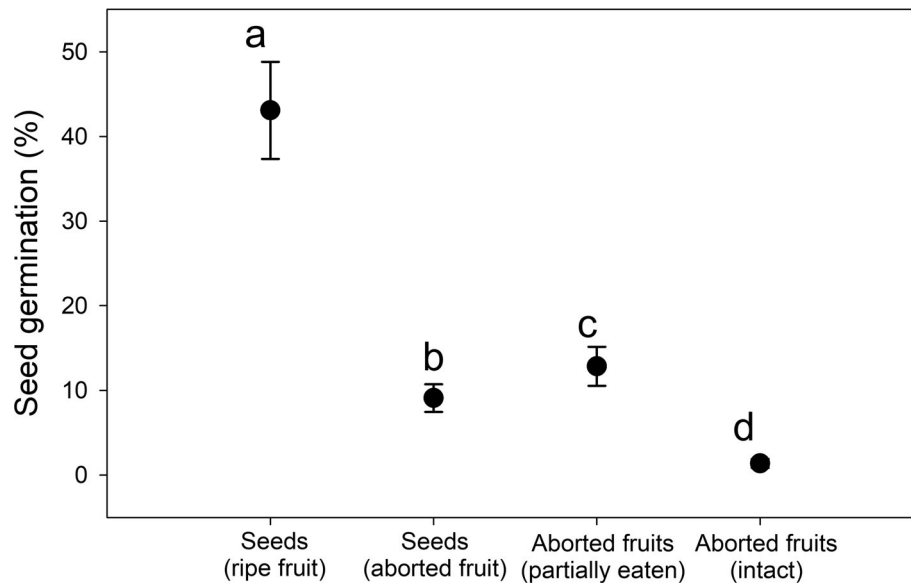
Fig. 4. Model-adjusted mean (± 1 SE) percentages of *Pyrus bourgaeana* seed germination for each of the four seed treatments (clean seeds from ripe fruits, clean seeds from intact aborted fruits, seeds within partially eaten aborted fruits, and seeds within intact aborted fruits). Different letters above bars denote significant ($P < 0.05$) differences among seed treatments.

after time (e.g., Boucher and Sork 1979, Stephenson 1980, Janzen 1983, Khan et al. 1999). Using a seed sowing experiment, we revealed that some seeds from *P. bourgaeana* aborted fruits are viable, germinating, and emerging seedlings in significant fractions. Paradoxically, however, these seeds are de facto unviable since they are confined within the extremely hard pericarp of aborted fruits, which prevents any seedling emergence and thus any contribution to tree recruitment. We show that only when rodents partially gnaw the pericarp walls of aborted fruits, seeds that escaped from rodent predation have the prospect of emerging and thus contributing to tree regeneration. Thus, in this and probably in many other similar synzoochorous systems, rodents act as rescuers of seeds confined within aborted fruits, conferring on the plants a largely overlooked benefit that could shape the reproductive strategy of many plant species.

Potential incidence of synzoochory in seeds from aborted fruits

Though the benefits for seed germination and seedling emergence derived from pericarp breakage of aborted fruits have not been evaluated

before in other synzoochorous systems, we predict that these benefits related and unrelated to seed movement are widespread. Firstly, dropping of immature fruits is a frequent process due to factors such as limited resources, inadequate pollination, pathogen attack, or herbivory (e.g., Boucher and Sork 1979, Bawa and Webb 1984, Traveset 1993, García et al. 1999, Young et al., 2007). The number of viable seeds in aborted fruits can be, as we demonstrated, substantial (e.g., Bawa and Webb 1984). For example, immature fruits of *Citrus sianensis* hold many germinable seeds several months before ripening, when they are only 23% of the size reached by fully developed fruits (Josep E. Peris, *personal communication*). Secondly, partial fruit consumption is also a commonplace process in both tropical and temperate habitats (e.g., Denslow and Moermond 1982, Bronstein and Hoffmann 1987, Bollen et al. 2004, Keuroghlian and Eaton 2009). Some of these partially gnawed fruits hold surviving seeds that are attractive to hoarding animals (e.g., Bollen et al. 2004, Fedriani et al. 2012), and thus, they are likely to be dispersed by seed hoarding animals worldwide. Finally, the neglected benefits of synzoochory likely are also

widespread when considering partially gnawed ripe fruits with hard pericarps. That is likely the case of many tropical species of Bignoniaceae, Capparidaceae, Chrysobalanaceae, and Lecythidaceae families (Kinzey and Norconk 1993, Peres and Baider 1997) as well as temperate species of Betulaceae, Coriariaceae, and Rosaceae families (Kalkman 2004, Kubitzki 2010, Pipinis et al. 2018). These benefits could be especially important in plant species producing thick hard fruit pericarps and multi-seeded fruits such as figs (Bronstein and Hoffmann 1987), citrus species (Peris 2020), some nut-producing species (Pipinis et al. 2018), and palms (Bradford and Smith 1977), as more seeds can potentially escape from predation. For example, Fedriani et al. (2012) demonstrated that partial consumption of fully developed ripe fruits by rabbits and small birds increased germination of surviving seeds and, subsequently, seedling emergence and survival in *P. bourgaeana* (see also Fedriani and Delibes 2013). Further studies are required to evaluate the pervasiveness across taxa and habitats of synzoochory in seeds from aborted fruits.

Demographic consequences of synzoochory in seeds from aborted fruits

Breakage of the pericarp of aborted fruits by rodents augmented germination and seedling emergence of seeds that escape from predation, and thus, it is a mechanism that would likely contribute to recruitment under field conditions. Since partially gnawed aborted fruits are usually hoarded by rodents nearby the mother tree (i.e., short-distance dispersal), this process is likely to increase local recruitment and thus the long-term tree population persistence (Fedriani et al. 2012, Jordano 2017). Effective local dispersal that increases local population size could indirectly promote more long-distance dispersal (and thus range expansion or colonization of new habitats) simply because the seed source is greater which results in more chances of long-distance dispersal events (Clark et al. 1988). Consequently, by rescuing seeds confined within aborted fruits, rodents provide an important service to *P. bourgaeana* and likely to many other plant species, but this has been neglected in recent reviews of synzoochory (Gómez et al. 2019).

Because aborted fruits tend to fall to the ground prematurely and, thus, their seeds are available to terrestrial consumers several months before the fall of ripe fruits, the fraction of their seeds rescued by rodents germinate and emerge seedlings much before than those from fully developed fruits. Early germination often enhances plant fitness by allowing early (and usually larger) seedlings to outcompete later (and usually smaller) seedlings (Verdú and Traveset 2005, De Luis et al. 2008). Furthermore, the sum of early seedlings from aborted fruits plus those emerged later from ripe fruits also diversifies the timing of seedling emergence (i.e., asynchrony), which may be advantageous in unpredictable conditions (Venable et al. 2008) such as those prevailing in Mediterranean ecosystems (Pugnaire and Valladares 2007, Fedriani and Delibes 2009). Since abortion of a large fraction of the crop is a widespread phenomenon (e.g., Lloyd, 1980, Janzen 1983, Fedriani et al. 2015), we propose that synzoochory of seeds from aborted fruits could be an integral part of many plants' reproductive strategies to ensure local persistence and not a mere by-product of optimizing resources allocation.

To conclude, we show that by gnawing aborted fruits and failing to depredate part of their developed seeds granivore rodents rescue many intrinsically viable seeds that are doomed to remain trapped and eventually die inside the hard pericarp. In this neglected modality of synzoochory, seed dispersers not only benefit mother plants by moving seeds within aborted fruits away but also by increasing their viability and thus enhancing seed germination and seedling emergence. As for other species interactions, synzoochory implies diverse costs and benefits for the interacting species, and we show that some of them have been unnoticed so far.

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