Interspecific competition for frugivores: population-level seed dispersal in contrasting fruiting communities

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Abstract

Indirect interactions among plant species mediated by frugivorous animals can be central to population and community dynamics, since the successful seed dispersal of species may depend on facilitative or competitive interactions with heterospecific plants. Yet, empirical evidence on these interactions is very scarce and mostly available at small spatial scales, within populations. Because lipid-rich fruits are known to be preferred by migratory birds, here we test our prediction of competitive inferiority of a carbohydrate-rich fruited species (the hawthorn *Crataegus monogyna*) compared to lipid-rich co-fruiting species in a Mediterranean region where the bulk of seed dispersal relies on migratory birds. We assessed avian seed dispersal in both relative (fruit removal rate) and absolute terms (seed dispersal magnitude) in seven hawthorn populations distributed across an altitudinal gradient encompassing three contrasting fruiting contexts: hawthorn is scarce in the lowlands, common in the midlands, and the dominant fruit species in the highlands. We found evidence of seed dispersal reduction due to interspecific competition in the lowland populations, where lipid-rich fruits dominate. Besides, DNA-barcoding analysis of bird-dispersed seeds revealed that only a small subset of the local frugivore assemblages consumed hawthorn fruits in the lowland communities. Instead, the consumers of hawthorn fruits resembled the local frugivore assemblages where hawthorn fruits were more dominant and frugivore choices more limited. Our study suggests mechanisms by which the rarity or dominance of plant species might be jointly influenced by environmental constraints (here, precipitation along the altitudinal gradient) and frugivore-mediated indirect interactions among plants hindering or facilitating seed dispersal.

Keywords: altitudinal gradient; *Crataegus monogyna*; frugivory; fruit removal; neighbourhood effects

Introduction

Species are embedded in complex webs of interactions, and the way species interrelate with each other has long attracted ecologists (Darwin 1859). Across trophic levels, direct interactions between species and indirect effects through interaction chains (e.g. '*a* → *b* → *c*'; species *a* can have indirect effects on species *c*, and vice versa, by affecting the abundance of species *b*) have been the focus of most studies aimed at understanding the role of interspecies relationships on population and community dynamics (Paine 1980; Hacker and Gaines 1997; Wootton 2002; Ripple and Beschta 2012). Within the same trophic level, however, indirect effects typically occur in the form of interaction modifications (e.g. '*a* → *c* & *b* → *c*'; resource species *a* can have indirect effects on resource species *b*, and vice versa, by increasing/decreasing the strength of its interactions with consumer species *c*) (Holt 1984; Wootton 1994; Roemer et al. 2002; Wootton 2002). Such effects are prevalent among co-occurring plant species sharing consumers and, owing to the sessile nature of plants, they are known as context or neighbourhood effects (Mack and Harper 1977; Carlo 2005). For instance, a flower species can receive more pollinator visits and enhance its seed production when growing surrounded by heterospecific flowers (e.g. Ghazoul 2006), while a seed species can increase its survival against seed predators if it is dispersed in an area dominated by heterospecific seeds (García et al. 2007). Both the consumer type (mutualistic or antagonistic) and the sign of the interaction modification will determine whether plant species interact through indirect facilitation or indirect competition (e.g. García et al. 2007; Yang et al. 2011; Martínez et al. 2014).

Seed dispersal is a pivotal process in plant population and community dynamics (Wang and Smith 2002; Levine and Murrell 2003). A substantial fraction of plant species across the world's biomes produce fleshy-fruits and rely on frugivorous animals for the dispersal of their seeds (Herrera 2002; Jordano 2014), thus, frugivores play an essential role in plant regeneration (Schupp et al. 2010). Because plant-frugivore systems are dominated by unspecific relationships (Herrera 2002), different plant species normally share disperser partners (e.g. Donoso et al. 2017). Thus, fleshy-fruited plants can affect the dispersal success of co-fruiting species by either increasing (facilitation) or decreasing (competition) their interaction strength with shared frugivores (Carlo 2005; Martínez et al. 2014; Albrecht et al. 2015). While facilitation may foster species diversity and coexistence (Carlo and Morales 2016; Morán-López et al. 2018a; Morán-López et al. 2018b), competition may lead to the dominance of the more attractive fruit species (Herrera 1984b; Izhaki 2002; Saracco et al. 2005). Diet complementation, i.e. the ingestion of fruit resources differing in nutritive content (Whelan et al. 1998) has been recently proposed as a behavioural mechanism of fruit choice facilitating the overrepresentation of rare species in bird-generated seed rains (Morán-López et al. 2018a). However, the study of nutritional ecology of fruit-eating birds has shown that fruit choices can be determined by the way in which nutrients are assimilated and metabolized (Levey and Martínez del Rio 2001). For instance, lipid-rich fruits are usually preferred by migratory birds that need to satisfy high energetic demands (Stiles 1980; Herrera 1982; Stiles 1993; Schaefer et al. 2014), and some species show digestive specialization to lipid-rich diets that appears to constrain the rate at which carbohydrate-rich fruits can be processed (Witmer and Van Soest 1998; Levey and Martínez del Rio 2001). Instead, the ingestion of carbohydrate-rich fruits has been reported to depress the efficiency of nutrient assimilation when switching to lipid-rich fruits (Afik and Karasov 1995; Levey and Martínez del Rio 2001). Accordingly, bird preferences for lipid-rich fruits have been suggested as an explanation for the lower fruit consumption rates found in populations of a carbohydrate-rich fruited species where lipid-rich fruits dominate (González-Varo 2010).

Yet studies addressing the effects of heterospecific neighbours on frugivore-mediated seed dispersal are still scarce and have yielded idiosyncratic results, suggesting a knowledge gap on the underlying mechanisms of facilitative or competitive interactions among co-fruiting species. Additionally, these previous studies have used experimental arrays (e.g. Carlo 2005; Xiao and Zhang 2016), simulations (Morán-López et al. 2018a; Morán-López et al. 2018b) or they have focused on intra-population effects at scales of a few meters around individual plants (e.g. Saracco et al. 2005; Martínez et al. 2014; Donoso et al. 2017). Thus, there is a lack of studies assessing indirect effects mediated by frugivores in multiple plant populations under contrasting heterospecific contexts (i.e. communities; but see Albrecht et al. 2015), and testing specific hypotheses about fruit nutritional content. This is surprising since the preferences (Stiles 1993; Levey and Martínez del Rio 2001; Carlo et al. 2003; Schaefer et al. 2014), routine movements (hundred of meters; González-Varo et al. 2017) and fruit-tracking behaviour (García and Ortiz-Pulido 2004; Tellería et al. 2008) of frugivorous birds suggest that indirect effects among co-fruiting plants must operate strongly at local and landscape scales (e.g., Herrera1984b; González-Varo 2010).

Here, we test the competitive inferiority of carbohydrate-rich fruits in a plant-frugivore system dominated by migratory birds. We used as a case study the hawthorn (*Crataegus monogyna* Jacq.) in south Spain, a woody plant species whose fruits are carbohydrate-rich in a Mediterranean region dominated by lipid-rich fruits. We assessed avian seed dispersal in seven hawthorn populations distributed across an altitudinal gradient encompassing contrasting heterospecific contexts: hawthorn is scarce in the lowlands, common in the midlands, and a dominant species in the highlands (Fig. 1). We expected reduced seed dispersal (i.e. increased competition) in contexts dominated by lipid-rich fruits. This would result in strong seed-dispersal differences across hawthorn populations and fleshy-fruited plant communities. Moreover, we assessed local bird assemblages and their relative contribution to hawthorn seed dispersal through DNA-barcoding analysis (González-Varo et al. 2014). Under a scenario of competitive inferiority of hawthorn plants surrounded by lipid-rich fruits, we expect seed-dispersal contributions to be only a small subset of the local frugivore assemblage, since most of the frugivore species would prefer to consume highly energetic lipid-rich fruits. By contrast, we expect hawthorn seed dispersers to match local frugivore assemblages where hawthorn is more dominant and, thereby, the frugivore community has little choice to manifest their preferences.

Material and Methods

Study species

The hawthorn (*Crataegus monogyna*, Rosaceae) is a common deciduous thorny shrub or small tree that grows up to 10-m in height, and is native to most of Europe, North Africa and West Asia (Christensen 1992). We focus on hawthorn as the study species, because its abundance in relation to co-occurring fleshy-fruited species (i.e. the heterospecific fruiting context) varies substantially with altitude in the study region (Fig. 1a; see sampling design below). Hawthorn fruits are red drupes (i.e. single seeded) with a water and carbohydrate-rich pulp that ripens during the late autumn (mean diameter = 9.2 mm, mean length = 9.7 mm, *n* = 1060 fruits from 53 individuals). The dry mass of the pulp only contains 2% of lipids, in contrast with the lipid-rich fruits of dominant Mediterranean plants in the lowlands, such as the lentisc (*Pistacia lentiscus*: 59%) and the wild olive tree (*Olea europaea* var. *sylvestris*: 42%) (Herrera 1987) (Fig. S1). Endozoochorous seed dispersal is mostly mediated by birds, which consume entire fruits and defecate or regurgitate intact seeds. The main dispersers of hawthorn seeds are thrushes (*Turdus* spp., Turdidae), with other small to medium-sized frugivorous birds belonging to families Sylviidae, Muscicapidae, Columbidae and Sturnidae playing a more minor role (Snow and Snow 1988; Martínez et al. 2008). Most of the *Turdus* species known to be seed dispersers of hawthorns in the Mediterranean regions are fully or partially migratory

(Tellería et al. 1999), which translates into high energetic demands and thus, the selection of lipid-rich fruits when choices of fruits are available (Stiles 1980; Bairlein 1990; Stiles 1993). Mammals only eat hawthorn fruits sporadically, thus, their contribution to the overall seed dispersal is negligible (Martínez et al. 2008; López-Bao and González-Varo 2011).

Study region and sampling design

The study region was located in Cádiz province (Spain), in the south of the Iberian Peninsula (Fig. 1a), a region where the relative abundance of hawthorns versus other co-occurring fleshy-fruited species varies substantially along an altitudinal gradient (Fig. 1a). In Mediterranean-climate regions, the highest hawthorn densities are typically found in mountainous areas, whose lower temperatures and higher annual precipitation buffer the drought conditions found in the lowlands (AEMET-IM 2011). Hawthorn thus occurs at low density in the lowlands (< 500 m a.s.l.), where Mediterranean sclerophyllous fleshy-fruited species are dominant, mainly lentiscs and wild olive trees. In contrast, hawthorn is the dominant fleshy-fruited species in the highlands of the nearby Sierra de Grazalema (~1000 m a.s.l.). Hence, the relative abundance of hawthorn fruits is very scarce in the lowlands, intermediate at mid elevations and dominant at the highlands (Fig. 1b; Fig. S1).

We conducted our study in seven hawthorn populations along the altitudinal gradient described above (Fig. 1b), aiming to represent three contrasting contexts of relative abundance of hawthorn fruits in the local fleshy-fruited plant communities: (*i*) 'scarce' (two populations), (*ii*) 'intermediate' (three populations), and (*iii*) 'dominant' (two populations). The percentage of hawthorn fruits in these population types was as follows: scarce: < 4.9%; intermediate: 16.8–52.4%; dominant: > 98.9% (see Table 1). We used this categorical approach because the studied populations not only differed in the relative abundance of hawthorn fruits but also in several relevant factors including the overall fruit availability (Fig. 2a) or the composition of heterospecific fruits (Table 1; Fig. S1).

The vegetation in the study populations consists of Mediterranean forests of large holm– (*Quercus ilex* subsp. *ballota*) and cork– (*Quercus suber*) oaks, and an understory dominated by treelets and shrubs. We obtained the local abundance of fruits from all fleshy-fruited species during the early hawthorn fruiting phenology by visually estimating the crop sizes of individual plants along a single transect crossing each of the study populations (e.g. López-Bao and González-Varo 2011). Transect areas (0.24–1.44 ha) varied owing to differences in both the transect length (120–650 m) and transect width (20–40 m) as a consequence of differences in local visibility (e.g. dense vegetation), accessibility (e.g. rocky outcrops in the highlands) and maximum distances among the studied hawthorn plants (higher in the 'scarce' populations, where hawthorn densities are very low).

Population-level seed dispersal: fruit removal rate and absolute magnitude

We assessed population-level seed dispersal through two different metrics, one relative (fruit removal rate) and one absolute (seed dispersal magnitude). Fruit removal rate (%) by legitimate seed dispersers was used as a surrogate for the relative seed dispersal (Simmons et al. 2018). We tagged between seven and ten individual hawthorns in each study population (total n = 53) in November 2014, at the beginning of the hawthorn fruiting season (2014–2015). In each individual, we randomly tagged four fruiting branches and counted all their fruits twice. We monitored an average of 151 fruits per individual and 1142 fruits per population, accounting for a total of 7994 fruits. We monitored fruit removal every three weeks until April 2015 (a total of eight surveys), when most fruits had either been removed or were dried on the branches. We considered any missing fruit (i.e. disappeared from the branch) between two consecutive surveys as removed by legitimate dispersers if the fruit stalks remained attached to the branches. The presence of stalks on the branches is a reliable indicator of consumption by legitimate seed dispersers because (*i*) when fruits fall to the ground through natural abscission or the action of wind or rain, their stalks fall with them (see Martínez et al. 2014; authors personal observations); and (*ii*) when fruits are pecked by pulp-pecking birds, the partially depulped seeds remain attached to the stalks on the branches or they fall to the ground with the stalks (authors' personal observations). Conversely, when standing fruits are removed by avian seed-dispersers, their stalks remain attached to the branch for a long time afterwards (see Martínez et al. 2014; authors personal observations). We thus counted the number of fruits and bare remaining stalks in successive surveys. After each survey, we removed the bare stalks with scissors to avoid recounting in subsequent surveys. For each individual hawthorn, we estimated its 'relative seed dispersal' as the percentage of fruit removal, by dividing the total number of bare stalks counted throughout the fruiting season by the initial number of fruits counted in the tagged branches.

The absolute numbers of fruits dispersed per unit area are probably more directly related to plant recruitment than estimates of the fraction of crops removed (Herrera 1984b) and, thus, more relevant for population and community dynamics (Garcia et al. 2005). Therefore, we estimated the magnitude of hawthorn seed-dispersal per unit area in the studied populations by multiplying the percentage of fruit removal measured in individual plants (i.e. relative seed dispersal) within each population by the local density of hawthorn fruits (i.e. fruits per hectare). As fruits are single-seeded, the magnitude of seed dispersal was expressed as the number of seeds successfully dispersed per hectare of each population.

Local disperser assemblages

To obtain the composition and abundance of avian frugivores in each of the seven studied populations, we performed bird censuses between late November 2014 and early April 2015, coinciding with the hawthorn fruiting season. We established one fixed-line transect of 40-m band (20-m band on each side) along each hawthorn population. Transect length varied among populations from 200 to 600 m owing to differences in accessibility (e.g. rocky outcrops in the highlands) and maximum distances among the studied hawthorn plants. Total sampling areas ranged between 0.8 and 2.4 ha. Censuses were repeated every 2–3 weeks, each consisting of the noting of all contacted birds – either audibly or visually – along each transect. We conducted between five and six censuses per population, giving a total of 37 censuses. Censuses were performed between 8.30 h and 13.00 h, on sunny or slightly cloudy days with low wind speed (<20 km h^{-1}).

Birds detected were subsequently categorized as (1) legitimate seed disperser, (2) seed/pulp predator, or (3) non-frugivorous species, according to their known effect when handling hawthorn fruits (Herrera 1984a; Snow and Snow 1988; Simmons et al. 2018). We then obtained the mean density of legitimate seed-dispersers in each population throughout the hawthorn fruiting phenology, expressed as number of birds per hectare. We also calculated the mean density of thrushes (*Turdus* spp.) in each population, given that they are known to be the main hawthorn seed-dispersers (Snow and Snow 1988; Martínez et al. 2008).

Hawthorn seed dispersers: DNA barcoding analysis

DNA of animal origin can be extracted from the surface of defecated or regurgitated seeds, allowing the identification of the animal species operating as legitimate seed dispersers (González-Varo et al. 2014). We conducted DNA barcoding analysis in bird-dispersed seeds sampled in the studied populations in order to identify the species of the local disperser assemblages that actually consumed hawthorn fruits. We placed a seed trap beneath the canopy of each study plant ($n = 53$) at the beginning of the study, each consisting of a plastic tray (40 × 55 × 8 cm) with small holes in the bottom (1 mm diameter) to allow the drainage of rainwater, and covered by wire mesh (1 cm light) to avoid predation (González-Varo et al. 2014; González-Varo et al. 2017). We counted all bird-dispersed seeds found in the traps in our periodical surveys, differentiating among hawthorn seeds and seeds belonging to other fleshy-fruited species (see Fig. S2). We sampled each bird-dispersed hawthorn seed (i.e. defecated or regurgitated) by placing it with a minimum of handling into a 2.0-mL sterile tube with the aid of the tube cap (González-Varo et al. 2014). Tubes were labelled and stored in a freezer at –20ºC until DNA extraction. We analysed an average of 14 hawthorn seeds per population, accounting for a total of 100 seeds out of the 133 found in the seed traps during the study.

For DNA extraction, we used a GuSCN/silica protocol, incubating each seed directly in extraction buffer (added to the 2.0-mL tube where the seed was sampled in the field). Disperser species identification is based on a 464-bp mitochondrial DNA region (COI: cytochrome c oxidase subunit I). We used the primers COI-fsdF and COI-fsdR for PCR amplification of this region, following the protocol described by González-Varo et al. (2014). We only sequenced one strand (forward primer) of the amplified COI fragments because in most cases the electrophoretic patterns were clear and resulting sequences (length: mean = 364 bp; median = 401 bp; range = 311–417 bp) allowed successful discrimination between disperser species. Sequences (i.e. barcodes) were aligned and edited using SEQUENCHER 4.9, and then identified using the 'BARCODE OF LIFE DATA' identification system (BOLD: http://www. boldsystems.org; Ratnasingham and Hebert 2007). BOLD accepts sequences from the 5′ region of the COI gene and returns species-level identification and assigns a percentage of similarity to matched sequences (for details, see González-Varo et al. 2014). Species identification was based on a 99.4–100% of sequence similarity.

Data analysis

We used generalised linear models (GLMs) to analyse differences between hawthorn fruiting contexts (i.e. ‘scarce’, ‘intermediate’ and ‘dominant’) in population-level seed-dispersal, both in relative (fruit removal rate; binomial distribution and logit link) and absolute terms (seed dispersal magnitude; negative binomial GLM). Fruit removal rates were thus modelled as a Bernoulli-distributed response variable (successes *vs*. failures). Seed dispersal magnitude was rounded and converted into integers (seeds ha^{-1}). We chose negative binomial GLM for analysing seed dispersal magnitude in order to solve the huge overdispersion found in a previously fitted Poisson GLM. We used a nested ANOVA design in both GLMs, including the fruiting-context type (i.e. ‘scarce’, ‘intermediate’ and ‘dominant’) as the main fixed factor and the population identity as a nested factor within context type (e.g. Traveset et al. 2012). This allowed us to calculate the percentage of explained deviance (ED) accounted by each variance component (fruiting context type and population nested within type) in order to evaluate their importance.

We used the Kendall’s rank correlation coefficient (τ) to test for monotonic associations between the mean density of avian seed-dispersers and the fruit removal rate in the studied hawthorn populations. We performed two different tests, considering the mean density of all avian dispersers and the mean density of thrushes (*Turdus* spp.), the main hawthorn dispersers. We performed two additional tests after weighting both avian densities (i.e. individuals ha^{-1}) by the local density of fleshy fruits (i.e. fruits ha^{-1}). This metric was expressed as ‘individuals per million of fruits’. We performed one-tailed tests because these relationships are expected to be positive; a lack of relationship would indicate that processes other than disperser limitation (e.g. interspecific competition) shaped hawthorn relative seed dispersal.

In those populations where lipid-rich fruits were not a limiting resource, we expected a selection of these highly energetic fruits by the frugivore community and hence, that the actual seed dispersal of hawthorn relayed only on a small subset of the local frugivore assemblage. To evaluate this, we used Kendall's rank correlation coefficient to test for a positive association between the number of disperser species identified through DNA barcoding and the fruiting context type of the populations (scored as 'scarce' = 1, 'intermediate' = 2, 'dominant' = 3; e.g. Moran et al. 2009). Moreover, we assessed similarity between the local disperser assemblage in each population (obtained through our bird censuses) and the set of dispersers that actually consumed hawthorn fruits (identified through DNA barcoding). We used the Jaccard's index to assess pairwise similarity in qualitative terms, and a proportional similarity index to assess pairwise similarity when accounting for the relative contribution of each disperser species. Jaccard's index was calculated as $J = c/(a + b - c)$; where *a* and *b* are, respectively, the number of disperser species in the local assemblage (*a*) and identified through barcoding in hawthorn seeds (*b*), whereas *c* is the number of disperser species shared by *a* and *b*. We calculated the proportional similarity index (PS; Hurlbert 1978) as: $PS = \sum_{i=1}^{n} min(p_{ia}, p_{ib})$; where for *n* species, p_{ia} is the relative contribution of the bird species *i* to the local disperser assemblage (*a*) and p_{ib} is the relative contribution of the bird species *i* to hawthorn seed dispersal (*b*). Both indices range from 0 (no overlap) to 1 (complete overlap). High Jaccard values indicate that most frugivore species recorded in the censuses were also identified through barcoding as legitimate hawthorn seed-dispersers, whereas high PS values indicate that frugivore species consumed hawthorn fruits proportionally to their local abundances. We thus hypothesised both similarity indices to be positively related to hawthorn dominance in the fruiting contexts. Where hawthorn is rare, high abundances of heterospecific fruits must foster frugivore-specific preferences towards highly energetic fruited-species, thereby hawthorn seed-dispersers are expected to be a small subset of the local frugivore assemblage. By contrast, in those populations where hawthorn fruits dominate, frugivorous birds have little choice so hawthorn seed-dispersers are expected to mirror the local frugivore assemblages. We also used Kendall's rank correlation coefficient to test for associations between both similarity indices and the fruiting context type of the populations. All statistical analyses were carried out with R version 3.3.3 (R Development Core Team 2015).

Results

Population-level seed dispersal

Local fruit densities, considering all fleshy-fruited species, ranged from 334,000 to 1,254,230 fruits ha^{-1} (Fig. 2a; Fig. S1), and were on average higher in ‘intermediate’ populations (841,440) than in ‘scarce’ (789,000) and ‘dominant’ populations (348,310 fruits ha^{-1}). Across populations, the local densities of hawthorn fruits ranged from 12,280 to 358,620 fruits ha^{-1} (Fig. 2a) and were on average much lower in ‘scarce’ than in ‘intermediate’ and ‘dominant’ populations (31,410 << 221,590 < 344,540 fruits ha^{-1}, respectively; estimates rounded to the nearest tenth).

We found a 6.6-fold difference in the mean fruit removal rate across populations, which ranged from 8.4 to 55.2% (Fig. 2b). Fruit removal rate varied significantly between hawthorn fruiting contexts, as well as among populations within them (Fig. 2b, Table 2), and both factors accounted for ~50% of the explained deviance (see Table 2). By fruiting context, the mean fruit removal rate was more than two times greater in the ‘intermediate’ populations (37.1%) than in the ‘scarce’ (17.1%) and ‘dominant’ ones (16.1%) (Fig. 2b). Frugivores in ‘intermediate’ and, particularly, in ‘scarce’ populations mostly ejected heterospecific seeds beneath the studied plants (see details in Fig. S2), indicating they mostly consumed fleshy fruits from species other than hawthorn. In contrast, most seeds ejected by frugivores in the ‘dominant’ populations were hawthorn seeds (see Fig. S2).

We found huge differences in the seed-dispersal magnitude across populations (Fig. 2c), which ranged from 2870 to 99,530 seeds ha^{-1} (estimates rounded to the nearest tenth). Such differences were driven by variation in both local fruit availability (Fig. 2a) and fruit removal rates (Fig. 2b). We found significant differences between hawthorn fruiting contexts and among populations within contexts, yet most of the explained deviance was accounted for by the fruiting context (89%; Table 2). The seed-dispersal magnitude was on average 17 and 13 times greater in the ‘intermediate’ (72,570 seeds ha^{-1}) and the ‘dominant’ populations (55,980 seeds ha^{-1}), respectively, than in the ‘scarce’ ones (4180 seeds ha^{-1}) (Fig. 2c). Notably, the ‘intermediate’ populations showed the highest magnitude of seed dispersal despite having, on average, a smaller density of hawthorn fruits (221,590 fruits ha^{-1}) than the ‘dominant’ populations (344,540 fruits ha^{-1}).

Local frugivores and hawthorn seed-dispersers

The local density of seed dispersers (all species) ranged from 4.2 to 35.8 birds per ha^{-1} (Fig. 3a) and was on average higher in the ‘scarce’ populations than in the ‘intermediate’ and the ‘dominant’ ones (25.3 > 15.4 > 8.2 birds per ha^{-1}, respectively). Indeed, the total density of seed dispersers decreased significantly as the hawthorn fruiting context increased ($\tau = -0.655$, $P = 0.027$, $n = 7$ populations). We recorded eight distinct bird species known to be hawthorn’s legitimate seed dispersers in our bird censuses: four species of thrushes (*Turdus merula*, *T. philomelos*, *T. iliacus* and *T. torquatus*) and four species of small passerines (*Erithacus rubecula*, *Sylvia atricapilla*, *S. melanocephala* and *Phoenichurus ochruros*) (Fig. 3b). At each population, we recorded 2–4 species of thrushes and 3–4 species of small passerines. The local density of thrushes ranged from 1.2 to 4.8 birds per ha^{-1} (Fig. 3a), and was on average higher in ‘scarce’ and ‘intermediate’ populations that in ‘dominant’ ones (3.6 = 3.6 > 2.8 birds per ha^{-1}, respectively). Notably, small passerines accounted for most individuals recorded across populations (Fig. 3b). Neither the total density of frugivores, the density of thrushes, nor both densities weighted by the local density of fruits (i.e. frugivore individuals per million of fruits), were significantly associated with fruit removal rates (all Kendall's $|\tau| \leq 0.43$, $P > 0.5$, $n = 7$ populations; see details in Fig. S3).

We successfully identified, through DNA barcoding, the disperser species for 87 out of the 100 seeds analysed. Unfortunately, all seeds analysed from population Sc2 produced non-specific amplifications, which prevented us from estimating the relative role of seed disperser species at this site. We identified through DNA barcoding eight distinct bird species in defecated or regurgitated hawthorn seeds (Fig. 3c), including seven species recorded in the bird censuses (all but *P. ochruros*) plus one thrush species that was not recorded visually (*T. viscivorus*). Notably, thrushes accounted for most barcoding identifications across populations (80%), confirming their key role as hawthorn seed-dispersers. The highest fractions accounted for by small passerines were found in 'dominant' populations (Fig. 3c). Rarefaction analyses revealed that the observed differences in disperser composition among populations were not a consequence of uneven sample sizes ($n_{\text{barcoded seeds}} = 7–22$; see Fig. S4).

The number of seed-disperser species identified through DNA barcoding increased nearly significantly along with the hawthorn fruiting contexts ($\tau = 0.585$, $P = 0.069$, $n = 6$; Fig. 4a), and was not correlated with the number of species recorded through bird censuses ($\tau = 0.277$, $P = 0.243$, $n = 6$; Fig. 4a). Moreover, we found a partial trend of increasing similarity between the composition of the local frugivore assemblages and the hawthorn seed-dispersers as the relative density of hawthorn fruits increased in the fruiting context (Fig. 4b), yet rank correlations were not significant (Jaccard: $\tau = 0.234$, $P = 0.269$; PS: $\tau = 0.389$, $P = 0.152$, $n = 6$). A clearer trend seemed to be prevented by the population Do2 (Fig. 4b) and both rank correlations became significant after excluding this 'dominant' population (Jaccard and PS: $\tau = 0.837$, $P = 0.026$, $n = 5$). The fact that one of the main dispersers identified through DNA barcoding in population Do2 (*Turdus viscivorus*) was not recorded through bird censuses (see Fig. 3b,c), together with the fact that this population had – by far – the lowest frugivore densities (see Fig. 3a), led us to suspect that our bird censuses could not have described properly the local frugivore assemblage at this site, and thereby we consider Do2 as an outlier.

Discussion

By combining several lines of evidence at the population and community level, our study supports the competitive inferiority of hawthorn fruits to obtain mutualistic services from avian frugivores when co-occurring with high-rewarding, lipid-rich fruits. We found no evidence of rare-biased seed dispersal (Carlo and Morales 2016); that is, an increased consumption of hawthorn fruits by frugivores in lipid-rich communities in order to complement their diet (Morán-López et al. 2018a). Conversely, we found decreased hawthorn seed-dispersal in communities dominated by lipid-rich fruits. Moreover, the contribution of frugivores to hawthorn seed dispersal varied between fruiting contexts according to a pattern of competitive inferiority: hawthorn seed-dispersers were more species-rich and resembled the local frugivore assemblage in communities where hawthorn was dominant and frugivore choices are limited, but they were less species-rich and only accounted for a small subset of the local frugivore assemblage in communities dominated by heterospecific fruits.

Population-level seed dispersal in contrasting fruiting communities

Here we estimated the seed dispersal success in the studied hawthorn populations through two complementary metrics: fruit removal rate (relative success) and seed dispersal magnitude per unit area (absolute success). Importantly, both metrics are highly dependent on local fruit abundance: a high fruit abundance can lead to a low fruit removal rate along with a high seed-dispersal magnitude (see Izhaki 2002; Carlo 2005). The rationale is that if fleshy fruits are not a limiting resource, the frugivore assemblage can be satiated and remove only a fraction of the available fruit crops, while the high abundance of fruits still implies a large number of seeds being dispersed per unit area (Hampe 2008). Indeed, this seems to be what happened in our 'dominant' populations (Fig. 2, see further discussion on this pattern below). Seed dispersal success at the population-level can be also determined by the abundance of the local frugivore assemblages (Herrera 1984b; Carlo et al. 2003; González-Varo 2010). These factors are – to some extent – interdependent since frugivores can track fruits at large spatial scales, being more abundant and active where fruits abound (García et al. 2001; García and Ortiz-Pulido 2004; Hampe 2008; Tellería et al. 2008). In addition, seed dispersal success can depend on the foraging preferences of frugivores (Carlo et al. 2003; González-Varo 2010; Schaefer et al. 2014; Morán-López et al. 2018a; Morán-López et al. 2018b).

In our study, the observed patterns of fruit removal rate and seed-dispersal magnitude across hawthorn fruiting contexts seem to respond to a combination of these factors. Fruit removal rates were on average higher in 'intermediate' populations and similarly low in both 'scarce' and 'dominant' populations (Fig. 2b). The higher rate in 'intermediate' populations may be due to the combination of a high density of seed dispersers in these sites (Fig. 3a) along with a more limited choice for heterospecific fruits than in 'scarce' populations (Fig. S1). Yet, the estimated seed-dispersal magnitude was similarly high in 'intermediate' and 'dominant' populations, and much lower in 'scarce' populations (on average 17 and 13 times lower, respectively; Fig. 2c). This pattern of similar seed-dispersal magnitude in 'intermediate' and 'dominant' populations can be explained by frugivore satiation in the 'dominant' populations (Hampe 2008). The high densities of hawthorn fruits in the 'dominant' populations along with the lowest densities of avian frugivores (Fig. 3a) resulted in the consumption of a small fraction of the available fruit crops. Nevertheless, such a low fruit removal rate resulted in a high amount of seeds dispersed per hectare due to the high local abundance of hawthorn fruits (see similar patterns in Carlo 2005). On the other hand, the low seed-dispersal success found in 'scarce' populations, both in relative and absolute terms, revealed a pattern of frugivore preferences towards heterospecific lipid-rich fruits. Three main lines of evidence support this idea. First, the composition of the seed species in the seed traps showed that frugivores mostly consumed heterospecific fruits in populations where lipid-rich fruits prevail (i.e. 'intermediate' but especially 'scarce' populations; see details in S2). This was revealing since the highest seed-rain densities of fleshy-fruited species typically occur beneath conspecific plants (e.g. Jordano and Schupp 2000; González-Varo et al. 2014), and we only placed seed traps beneath hawthorns. Second, we found no positive associations between hawthorn fruit removal rate and various metrics of local frugivore abundance, including bird densities weighted by local fruit abundance (Fig. S3). In fact, the local density of seed dispersers was on average higher in 'scarce' populations (Fig. 3a), the ones with the lowest seed-dispersal success. Third, DNA-barcoding identifications showed frugivores' contributions to hawthorn seed dispersal were more species rich and resembled more to the local frugivore assemblages where hawthorn dominance increased and, thus, frugivore choices were limited (Fig. 4b). Therefore, only a small subset of the local frugivore assemblages dispersed hawthorn seeds in communities where hawthorn fruits were scarce. This is expected to have functional consequences since disperser richness is positively related with the diversity of habitats and microhabitats of seed deposition (e.g. Jordano and Schupp 2000; García and Martínez 2012; González-Varo et al. 2017). These three lines of evidence support the competitive inferiority of the hawthorn's carbohydrate-rich fruits versus the high energetic lipid-rich fruits of co-fruiting species, and explain the poor dispersal observed in 'scarce' populations.

One might think that fruit size was an important driver of the observed patterns for seed-dispersal success because the size of hawthorn fruits (mean diameter = 9.2 mm) could restrict ingestion by small passerines, whose gape width (~7–8 mm) is narrower than that of thrushes (~11–13 mm) (Herrera 1984a). However, we discarded this idea since, for example, the abundant blackcaps (*Sylvia atricapilla*) have strong preferences for the similarly sized wild olives (mean diameter = 9.0 mm) (González-Varo et al. 2017). Moreover, the DNA-barcoding results showed that intraspecific variability in fruit diameter can allow small passerines to consume the smaller hawthorn fruits (Fig. S5; see also González-Varo and Traveset 2016). Finally, population-level fruit removal rates were not correlated with fruit diameter (Fig. S5).

Relevance for community dynamics along an environmental gradient

This study shows that the nutrient composition of the fruiting community can influence frugivore foraging choices, resulting in a competitive disadvantage for the less-preferred plant species. In our study system, where most fruit removal relies on migratory birds, lipid-rich fruits are preferred (Schaefer et al. 2014). Contrary to what has been suggested to explain the persistence of rare plant species in communities (Morán-López et al. 2018a; Morán-López et al. 2018b), our results indicate that, when the hawthorn is rare in a community where lipid-rich fruits are dominant, frugivores do not show a rare-biased fruit choice. Conversely, the frugivores' preferences towards lipid-rich fruits will promote an underrepresentation of hawthorn in the seed rain (see Fig. S2).

Besides differing in their local fruiting context and seed dispersal success, the hawthorn populations studied are also subjected to the abiotic factors inherent to the altitudinal gradient where they occur. In Mediterranean ecosystems, soil moisture – especially during summer – determines survival and growth of hawthorn seedlings, which overall benefit from wet conditions (Matías et al. 2011; Matías et al. 2012). Accordingly, hawthorn seedlings face harsher conditions for successful recruitment at 'scarce' populations located in the lowlands, where the mean annual rainfall does not exceed 600 mm (AEMET-IM 2011). This is compared to seedlings at 'intermediate' and 'dominant' populations, where mean annual rainfall ranges between 1000-1400 mm (AEMET-IM 2011). This deciduous temperate species is scarce in warm Mediterranean lowlands because it is in the periphery of its climatic niche, thus hawthorn rarity is linked to environmental variation (Guo et al. 2005). The lowland hawthorn populations seem to be in a position of competitive inferiority to sclerophyllous Mediterranean plants (e.g. lentiscs, wild olive trees), not only due to their disadvantage in attracting frugivores' dispersal services, but also for their limited ability to cope with summer drought. Our sampling design highlights the importance of environmental variation at a regional scale in determining dominance or rarity of plant species (Guo et al. 2005), which in turn may influence frugivore-mediated interactions affecting plant species fitness via successful seed dispersal (Levine and Murrell 2003; see also Bimler et al. 2018).

Conclusions: a matter of scale

Until now, frugivore-mediated indirect interactions have mostly been studied at the neighbourhood scale, i.e. within a few meters around focal plants within a given population (Carlo 2005; Saracco et al. 2005; Martínez et al. 2014). Hence, there is a lack of empirical studies like ours comparing multiple populations embedded in contrasting fruiting communities (Herrera 1984b; González-Varo 2010). The local scale (i.e. 10^2–10^3 m) is the main spatial scale at which relationships between woody plants and avian frugivores occur (e.g. Jordano et al. 2007; González-Varo et al. 2017), as well as many other local processes affecting population and community ecology (Levine and Murrell 2003). Covering this scale in empirical studies is sometimes challenging and this may explain why the scant evidence on interspecific competition for frugivores' services has been mainly focused at narrower scales in the literature. Here, we shed light onto frugivore-mediated indirect interactions across plant populations. We show evidence of the drivers leading to indirect competitive inferiority of carbohydrate-rich fruited species in Mediterranean plant communities dominated by lipid-rich fruits, and our findings may be extrapolated to many other systems where the bulk of seed dispersal relies on migratory birds (e.g. González-Varo 2010). Yet, more empirical research is needed to better understand how frugivore-mediated indirect interactions shape community dynamics, particularly along environmental gradients that influence plant species rarity or dominance.

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Table 1. Characteristics of the studied hawthorn (*Crataegus monogyna*) populations. Hawthorn fruiting contexts refer to the relative abundance of hawthorn fruits in the local fleshy-fruited plant communities. FFS: fleshy-fruited species. *Cm*: *Crataegus monogyna*; *Hh*: *Hedera helix*; *Oe*: *Olea europaea* var. *sylvestris*; *Pl*: *Pistacia lentiscus*. Details on the entire composition of fleshy-fruited communities and information on pulp constituents are provided in Fig. S1.

Fruiting context	Population (code: name)	Altitude (m a.s.l.)	Coordinates (decimal degrees)	Sampling area (ha)	Hawthorn fruits (%)	Dominant FFS
Scarce	Sc1: Garrapilos	50	36.660°, –5.949°	2.4	4.9	*Pl*, *Oe*
Scarce	Sc2: Abiertas	250	36.753°, –5.711°	1.3	2.2	*Oe*, *Pl*
Intermediate	In1: Benamahoma	520	36.769°, –5.457°	1.1	26.1	*Pl*, *Cm*
Intermediate	In2: Gaidovar	765	36.770°, –5.357°	1.6	16.8	*Oe*, *Cm*
Intermediate	In3: Villaluenga	960	36.694°, –5.378°	1.0	52.4	*Cm*, *Oe, Hh*
Dominant	Do1: Boyar	1105	36.755°, –5.396°	0.8	98.9	*Cm*
Dominant	Do2: Embalse	1010	36.766°, –5.380°	1.1	99.8	*Cm*

Table 2. Results of the nested GLMs analysing differences between hawthorn fruiting contexts (‘scarce’, ‘intermediate’, ‘dominant’) and among populations within each context type in ‘fruit removal rate’ (% removed by avian seed dispersers; binomial family and logit link) and ‘seed dispersal magnitude’ (number of fruits/seeds removed per hectare; negative binomial GLM). ‘ED (%)’ is the percentage of the total explained deviance accounted by each predictor variable.

Response variable	R^2_{GLM}	Predictor variables	df	*F*	*P*	ED (%)
Fruit removal rate	0.516	Hawthorn fruiting context	2, 50	237.6	< 0.001	50.3
		Population (within context)	4, 46	117.2	< 0.001	49.7
Seed dispersal magnitude	0.710	Hawthorn fruiting context	2, 50	61.7	< 0.001	89.2
		Population (within context)	4, 46	3.7	0.005	10.8

Figure captions

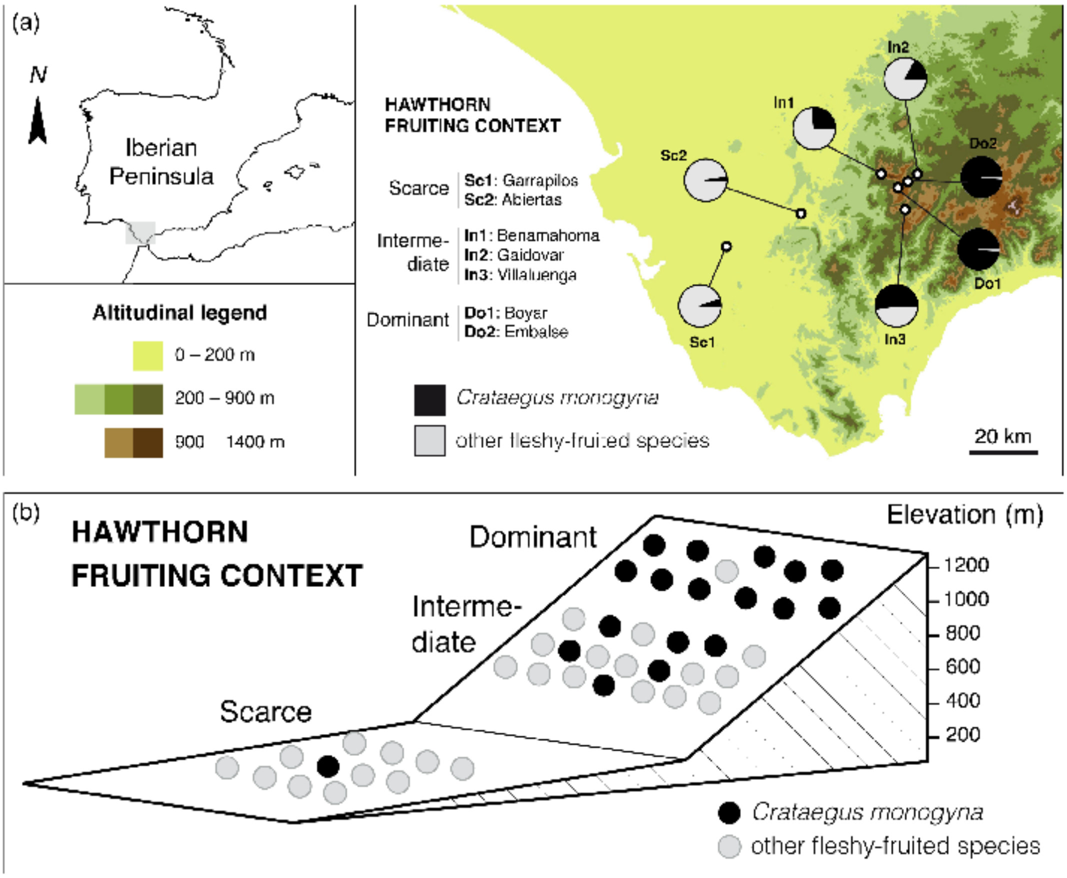
Figure 1. (a) Study region in the south of the Iberian Peninsula and geographic location of the studied hawthorn (*Crataegus monogyna*) populations. Pie charts denote the relative abundances of hawthorn fruits as well as of fruits belonging to other fleshy-fruited species in the populations (b) Sampling design of the study, with different population types in relation to the hawthorn fruiting contexts along an altitudinal gradient.

Figure 2. (a) Local fleshy fruit densities of all species (horizontal lines) and hawthorn (*Crataegus monogyna*: circles) during the autumn-winter 2014–2015 in the study populations. (b) Fruit removal (%) by avian seed dispersers and (c) estimated seed dispersal magnitude (seeds ha^{-1}) in the studied hawthorn populations. In (b) and (c), dashed lines denote means by hawthorn fruiting contexts, bars and shaded areas denote 95% CIs, whereas different capital letters denote significant differences ($P < 0.05$) between fruiting contexts (i.e. non-overlapping 95% CIs).

Figure 3. (a) Mean densities of all species of avian seed dispersers (horizontal lines) and thrushes (*Turdus* spp.; the main dispersers of hawthorn seeds: circles) during autumn-winter 2014–2015 in the study populations. (b) Relative abundance (%) of the different species of seed dispersers obtained through bird censuses (c) Relative contribution to dispersal of hawthorn (*Crataegus monogyna*) seeds (DNA barcoding identifications from defecated/regurgitated seeds) by distinct species. The full species names are *Turdus merula* (*Tm*), *T. viscivorus* (*Tv*), *T. philomelos* (*Tp*), *T. iliacus* (*Ti*), *T. torquatus* (*Tt*), *Sylvia atricapilla* (*Sa*), *S. melanocephala* (*Sm*), *Erithacus rubecula* (*Er*) and *Phoenichuros ochruros* (*Po*).

Figure 4. (a) Species richness of avian seed dispersers recorded at each site through bird censuses (horizontal lines) and identified through DNA barcoding in defecated/regurgitated hawthorn seeds (circles). (b) Similarity, in qualitative (Jaccard’s index: circles) and quantitative (PS index: triangles) terms, between the local assemblage of avian seed-dispersers (Fig. 3b) and the subset contributing to hawthorn seed dispersal (Fig. 3c)

Fig. 1



(a)
N
Iberian Peninsula
Altitudinal legend
0 – 200 m
200 – 900 m
900 – 1400 m
HAWTHORN FRUITING CONTEXT
Scarce
Sc1: Garrapilos
Sc2: Abiertas
Interme-diate
In1: Benamahoma
In2: Gaidovar
In3: Villaluenga
Dominant
Do1: Boyar
Do2: Embalse
Crataegus monogyna
other fleshy-fruited species
In2
In1
Sc2
Do2
Do1
Sc1
In3
20 km
(b)
HAWTHORN FRUITING CONTEXT
Dominant
Interme-diate
Scarce
Elevation (m)
1200
1000
800
600
400
200
Crataegus monogyna
other fleshy-fruited species

Fig. 2

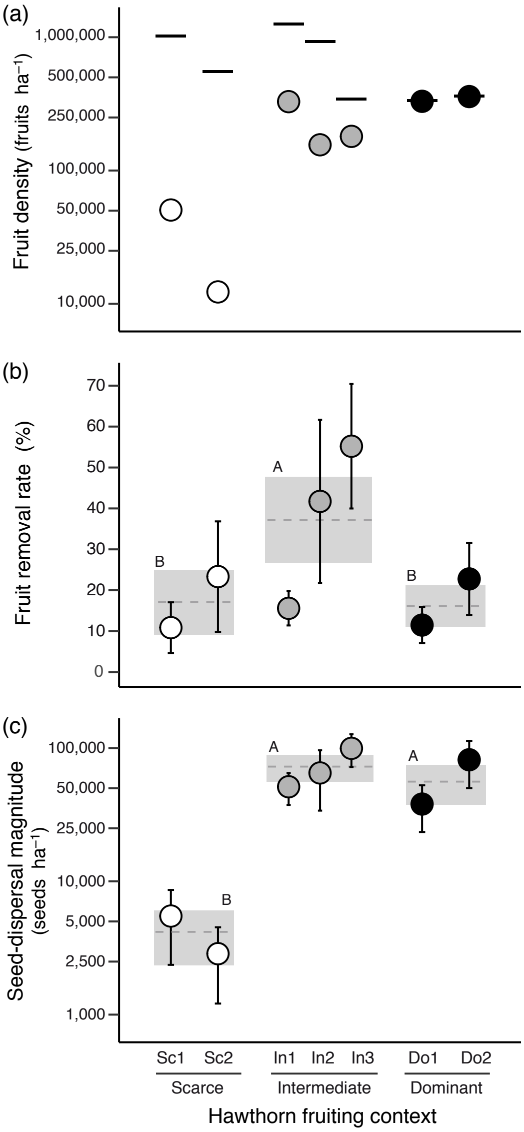

(a)
Fruit density (fruits ha−1)
1,000,000
500,000
250,000
100,000
50,000
25,000
10,000
(b)
Fruit removal rate (%)
70
60
50
40
30
20
10
0
A
B
B
(c)
Seed-dispersal magnitude (seeds ha−1)
100,000
50,000
25,000
10,000
5,000
2,500
1,000
A
A
B
Sc1
Sc2
In1
In2
In3
Do1
Do2
Scarce
Intermediate
Dominant
Hawthorn fruiting context

Fig. 3

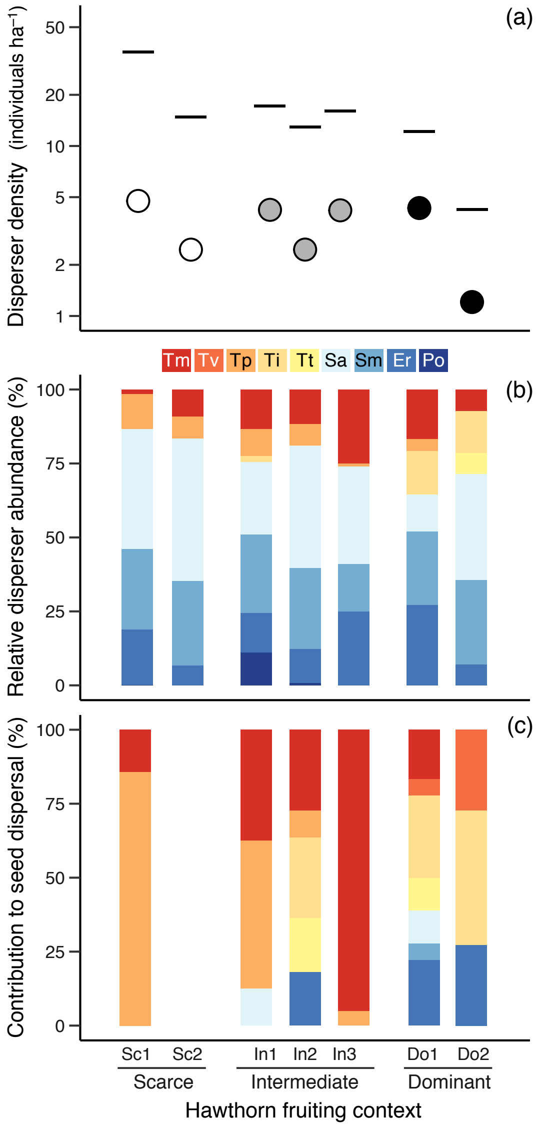
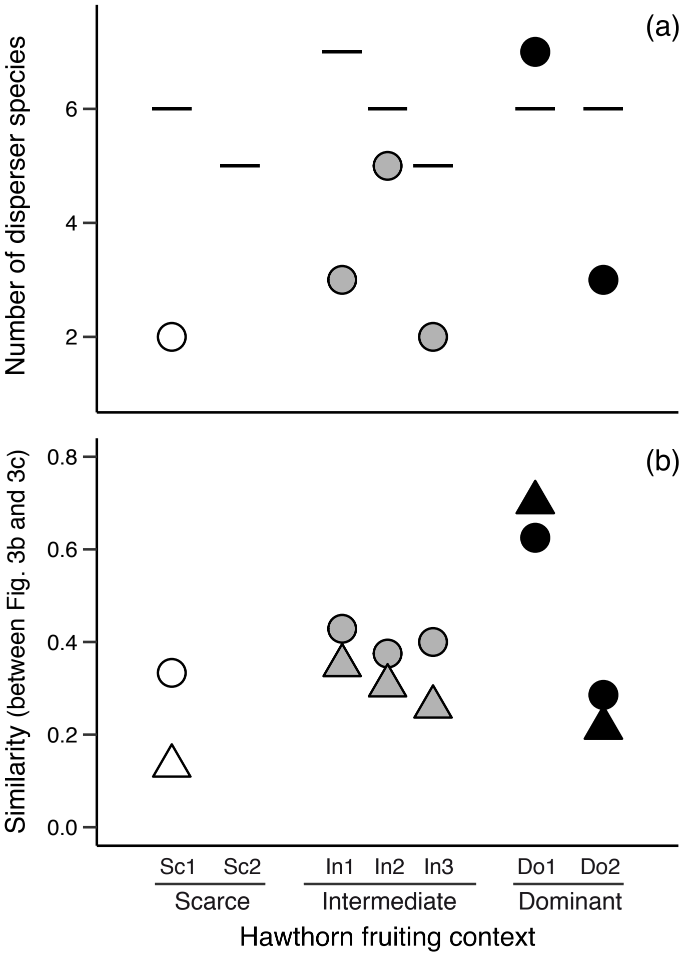

(a)
Disperser density (individuals ha⁻¹)
50
20
10
5
2
1
Tm
Tv
Tp
Ti
Tt
Sa
Sm
Er
Po
(b)
Relative disperser abundance (%)
100
75
50
25
0
(c)
Contribution to seed dispersal (%)
100
75
50
25
0
Sc1
Sc2
In1
In2
In3
Do1
Do2
Scarce
Intermediate
Dominant
Hawthorn fruiting context

Fig. 4


(a)
Number of disperser species
2
4
6
(b)
Similarity (between Fig. 3b and 3c)
0.0
0.2
0.4
0.6
0.8
Sc1
Sc2
In1
In2
In3
Do1
Do2
Scarce
Intermediate
Dominant
Hawthorn fruiting context

Interspecific competition for frugivores: population-level seed dispersal in contrasting fruiting communities

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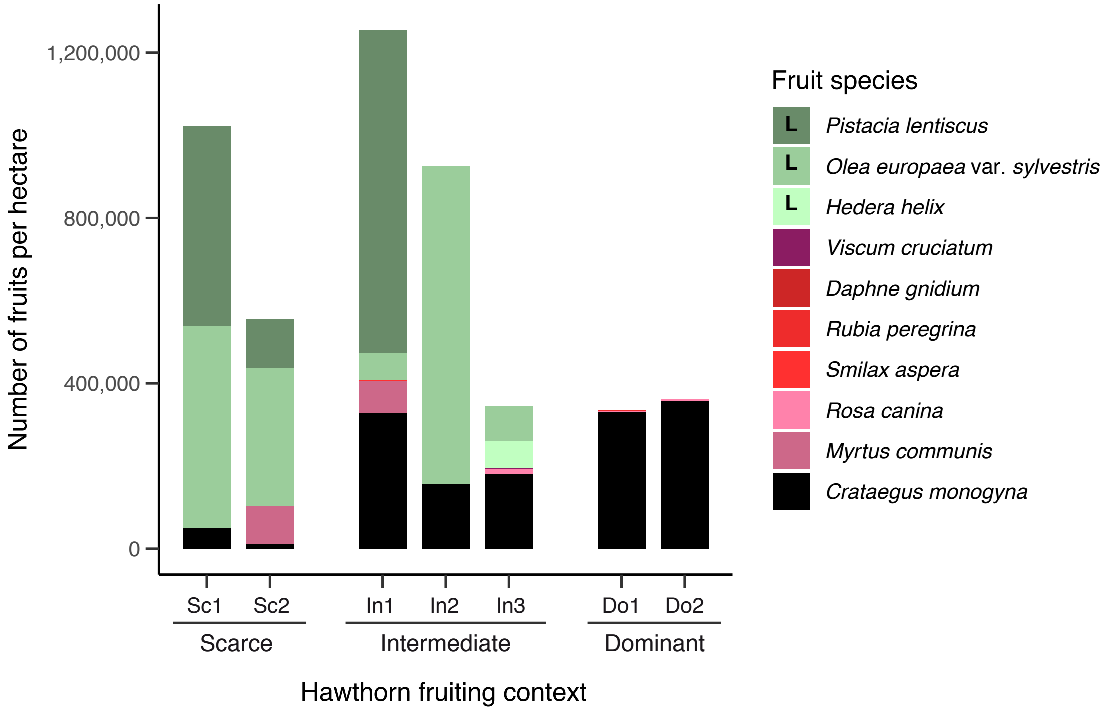
Electronic Supplemental Material (ESM)

Contents

Figure S1. Local abundance of fruits from all fleshy-fruited species during the early fruiting phenology of hawthorn (*Crataegus monogyna*) at the seven studied populations. Green colours and capital 'L' indicate lipid-rich fruited species (>30 % of their pulp constituents), whereas reddish colours indicate carbohydrate-rich fruited species. *Crataegus monogyna* has been highlighted in black. Percentage of lipids/NCS (non-structural carbohydrates) in relation to dry mass of pulp as follows: *Pistacia lentiscus*: 58.8/25.8, *Olea europaea*: 41.9/33.3, *Hedera helix*: 31.9/47.4, *Viscum cruciatum*: 14.3/60.2; *Daphne gnidium*: 2.6/80.5, *Rubia peregrina*: 9.9/64.5, *Smilax aspera*: 2.1/68.5, *Rosa canina*: 2.8/72.5, *Myrtus communis*: 2.0/70.2, *Crataegus monogyna*: 2.3/72.4 (Herrera 1987).

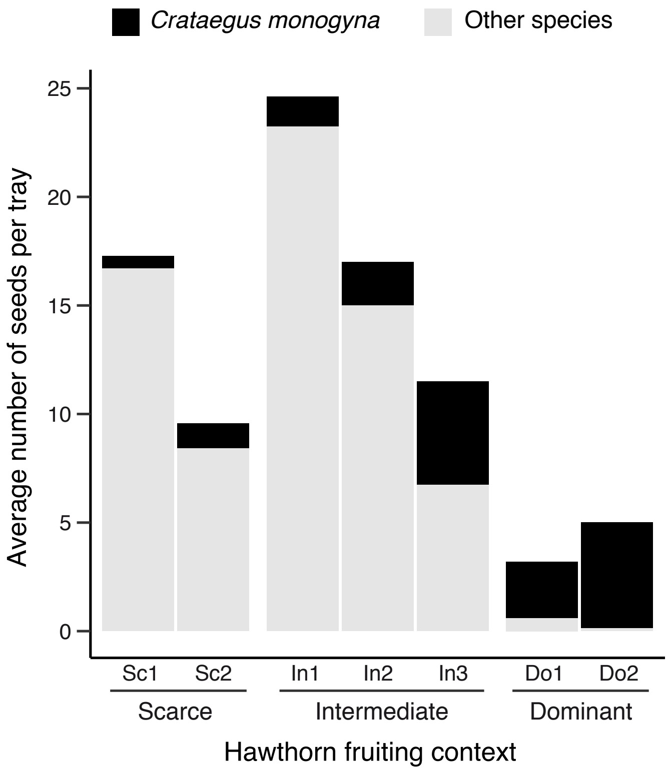


Reference

Herrera CM (1987) Vertebrate-dispersed plants of the Iberian Peninsula: A study of fruit characteristics. Ecol Monogr 57:305-331. doi: 10.2307/2937089

Figure S2. Average number of bird-dispersed seeds in the trays placed beneath the focal hawthorn plants (*Crataegus monogyna*) in the studied populations, differentiating between hawthorn seeds and seeds belonging to other fleshy-fruited species. We sampled a total of 133 hawthorn seeds and 513 seeds from other species. The average number of hawthorn seeds increased as heterospecific fruiting contexts decreased (0.9, 2.8 and 3.5 seeds per tray in the 'scarce', 'intermediate' and 'dominant' populations, respectively), as well as the percentage in relation to the total (6.4%, 15.6% and 89.5%, respectively).

Note: This figure does not represent seed-rain patterns because seed deposition was only assessed beneath the studied hawthorn plants and it is well known that the highest seed-rain densities of fleshy-fruited species typically occur beneath conspecific plants (e.g. Jordano and Schupp 2000; González-Varo et al. 2014). Thus, these patterns are expected to be highly hawthorn-biased. For instance, in population Sc1 hawthorn seeds accounted for 3.3% of all seeds found beneath hawthorn plants, but, when in this same population seed traps were placed beneath 'neutral' perches (i.e. non-fleshy-fruited trees and shrubs; González-Varo *unpublished data*), hawthorn seeds only accounted for 0.13% (1 of 726 seeds) of all seeds found during the hawthorn fruiting season.



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González-Varo JP, Arroyo JM, Jordano P (2014) Who dispersed the seeds? The use of DNA barcoding in frugivory and seed dispersal studies. Methods Ecol Evol 5:806-814. doi: 10.1111/2041-210X.12212

Jordano P, Schupp EW (2000) Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. Ecol Monogr 70:591-615

Figure S3. Relationships between fruit removal rate (%) at the population–level and (a) the local density of seed dispersers; (b) the number of dispersers per million of fruits; (c) the local density thrushes (*Turdus* spp.; the main dispersers of hawthorn seeds); and (d) the number of thrushes per million of fruits. Kendall's tests are shown in the panels. White, grey and black dots denote, respectively, 'scarce', 'intermediate' and 'dominant' hawthorn fruiting contexts. These results show that fruit removal rate at the population–level was not positively associated to the local abundance of dispersers or to disperser abundance weighted by the local fruit availability.

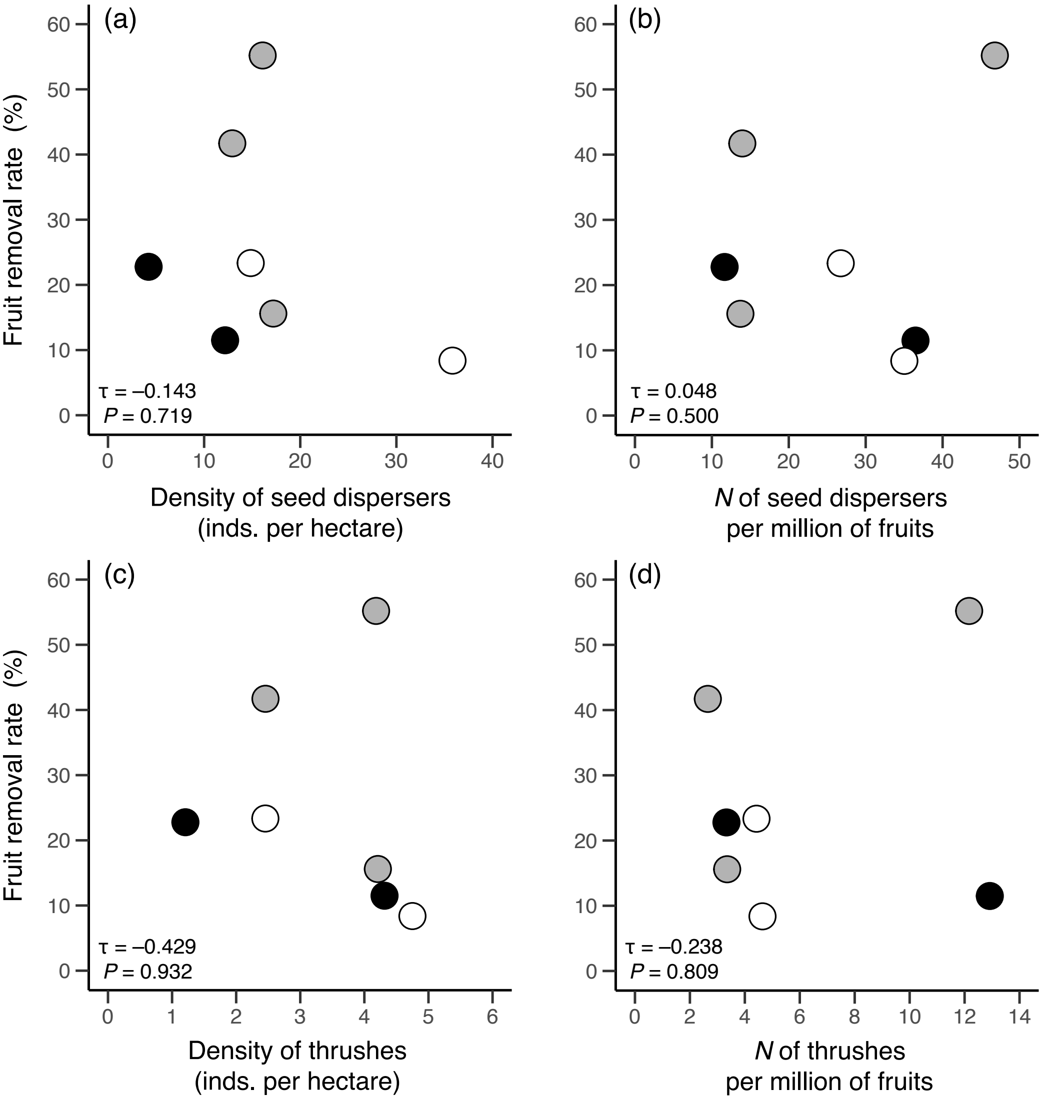

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Figure S4. (a) Species accumulation curves (SAC) assessing the robustness of DNA barcoding characterization of the seed dispersers of *Crataegus monogyna* in the studied populations. We used a random accumulator function (function *specaccum* in the R package *vegan* v.2.4–1; Oksanen et al. 2013), which finds the mean SAC and its standard deviation from random permutations (n = 100) of the data when accumulating individuals (here, bird-dispersed seeds; method = 'rarefaction') (Gotelli & Colwell 2001). We started with a vectorized matrix representing the bird species (rows) recorded during a cumulative number of DNA barcoded seeds (columns). This procedure plots the accumulation curve for the expected number of bird species identified through DNA–barcoding with increasing sampling effort. In each panel, the population code and the heterospecific fruiting context is shown. Red lines show the number of bird species estimated for the minimum sample size (i.e. n = 7 seeds in Sc1).

(b) We found a lack of relationship between the total sample size (i.e. n of barcoded seeds) and the total number of species identified (left panel), however, we found a strong relationship between the estimated number of species identified in 7 seeds (i.e. the minimum sample size) and the number of species identified using the total sample size (right panel). Kendall's tests are shown in both panels. White, grey and black dots denote, respectively, 'scarce', 'intermediate' and 'dominant' hawthorn fruiting contexts. Taken together, these results indicate that the differences among hawthorn populations in disperser assemblages characterised through DNA barcoding were not driven by differences in sample size.

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Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol Lett 4:379-391

Oksanen J, Blanchet FG, Friendly M, Roeland K, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2016) Vegan: Community Ecology Package. https://CRAN.R-project.org/package=vegan.

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Figure S4.

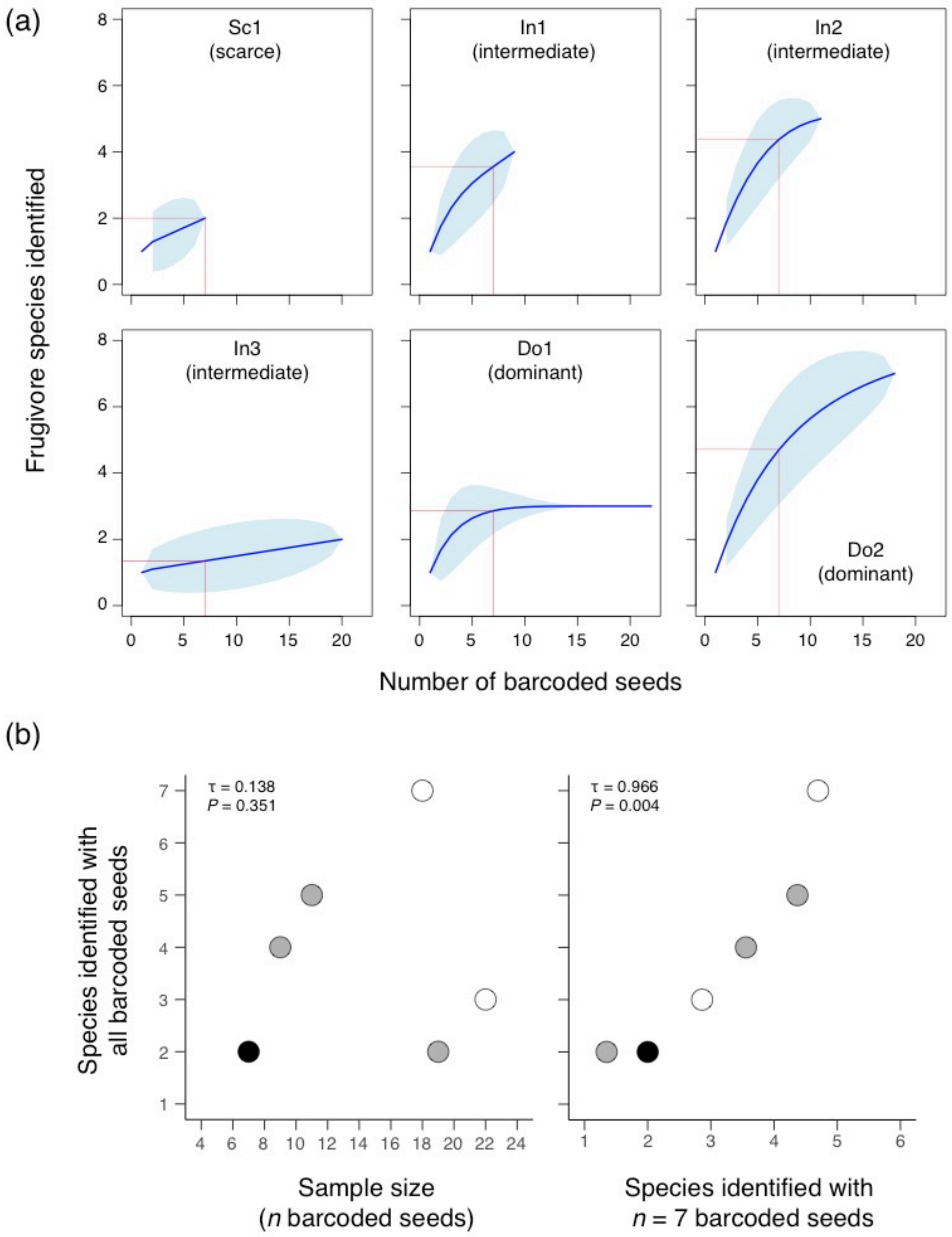

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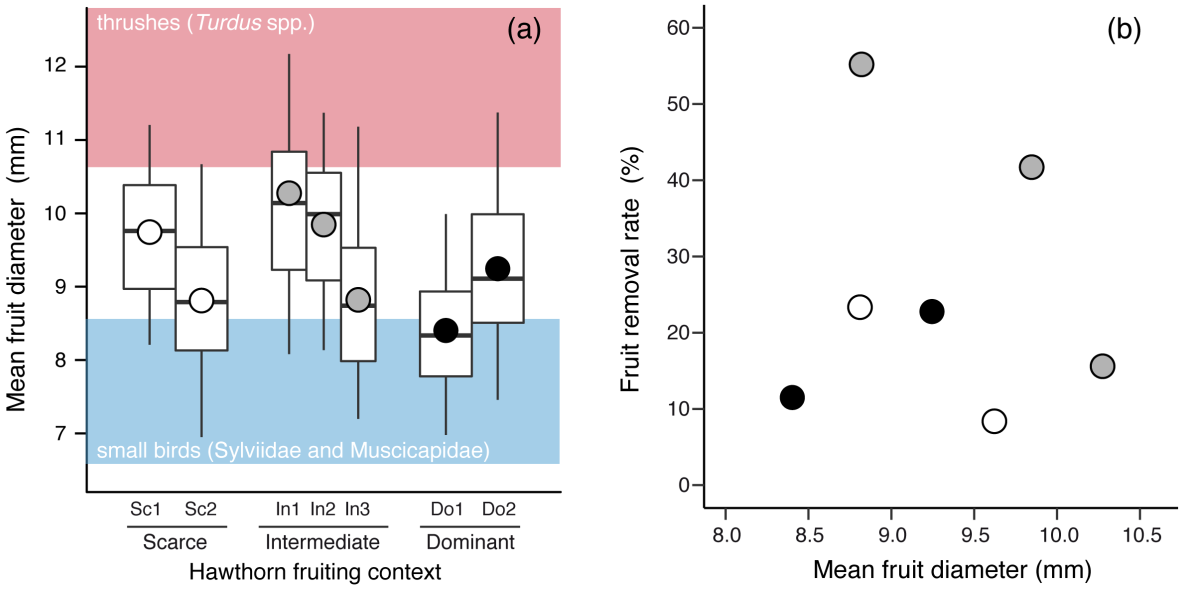
Figure S5. (a) Boxplot (median, quartiles and percentiles 2.5 and 97.5) showing variation in fruit diameter across the studied hawthorn populations (20 fruits per plant in 7–10 plants per population; total *n* = 1060 fruits). White, grey and black dots denote, respectively, ‘scarce’, ‘intermediate’ and ‘dominant’ hawthorn fruiting contexts. The red and blue areas denote the range in gape width (mm) among the studied thrushes (*Turdus* spp.) and small birds (Sylvidae and Muscicapidae), respectively (data from González-Varo and Traveset 2016 and Pigot et al. 2016). (b) Relationship between the population-level seed dispersal success (% fruits removed by avian seed dispersers) and the population mean fruit diameter (Kendall’s τ = –0.048. *P* = 0.500). Colour codes as in panel (a).



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