**Strong among population variation in frugivory strength by functional diverse frugivores: a
'reciprocal translocation' experiment¹**

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Abstract

Fruit-frugivore interactions are critical for the dynamics and evolution of many plant communities. The strength of the interactions between a given plant species and different frugivore guilds (e.g. seed dispersers, seed predators) often vary in space due to changes in extrinsic factors (e.g. frugivore abundances) and plant traits (e.g. fruit size and reward). By reciprocally translocating *Pyrus bourgaeana* ripe fruits representative of five Mediterranean localities during two consecutive years, we experimentally quantified guild-specific variations among populations in frugivory strength, while accounting for plant intrinsic and extrinsic factors. Though overall fruit removal did not differ among localities, there were strong guild-specific differences in fruit removal strength. Fruit removal by pulp feeders, seed dispersers, and fruit predators varied among populations up to 8.5-, 5.6-, and 4.0-folds, respectively. These strong variations seemed mediated by changes in frugivore relative abundances rather than on availability of alternative fruits. As expected, all fruit traits considered (e.g. fruit size, pulp amount) markedly varied among tree populations. However, no frugivore guild showed preference for fruits from any locality, suggesting that fruit traits did not contribute much to differences in frugivory strength among populations. Since the functional diverse frugivore guilds played contrasting roles in *P. bourgaeana* dynamics (e.g. seed dispersal vs. seed predation), our study highlights the importance of accounting for functional diversity in frugivore guilds when estimating spatial variations in seed dispersal. This investigation also illustrates a neglected but widely applicable experimental approach to identify the relative importance of extrinsic factors and fruit traits in mediating fruit-frugivore interactions.

Key words: endozoochory, fruit reward, functional diversity, interaction strength, pulp feeding, seed dispersal/predation, spatial variations

24 **Introduction**

25 Fruit-frugivore interactions are critical for the dynamics, evolution and conservation of many plant
26 communities worldwide (Levey et al. 2002, Bronstein et al. 2007, Fleming and Kress 2013, Bascompte
27 and Jordano 2014). Vertebrate frugivores obtain necessary nutrients and water from fleshy-fruits and,
28 in exchange, often provide the plants with seed dispersal services. The intensity and the nature
29 (mutualistic, antagonistic) of plant-frugivore interactions are highly variable both in space and time due
30 to a myriad of factors (Bronstein et al. 2007, Schupp et al. 2010, Fedriani et al. 2012, Perea et al. 2013),
31 including changes in the abundance of different frugivore guilds (e.g. seed dispersers, pulp feeders,
32 seed predator; Jordano and Schupp 2002, Fedriani and Delibes 2013). Despite the ecological and
33 evolutionary importance of these interactions, an understanding of the factors explaining guild-specific
34 changes in the frequency of fruit-frugivore interactions is lacking for most systems.

35 Variation in the frequency of the interaction between a given plant species and different
36 frugivore guilds potentially depends on a variety of intrinsic plant traits and extrinsic environmental
37 factors. Intrinsic traits include crop size, fruit size, and fruit reward (i.e. pulp quantity) and defenses
38 (Cipollini and Levey 1997, Guimarães et al. 2008, Lomáscolo et al. 2010, Galetti et al. 2013, Whitehead
39 et al. 2016). For instance, frugivores generally forage more intensely on plants producing large and
40 highly rewarding fruits (e.g. Parciak 2002, Blendinger et al. 2008, Pegman et al. 2016). Extrinsic factors
41 include the abundance of diverse frugivore guilds, the availability of alternative foods, and the risk of
42 predation perceived by frugivores (e.g. Carlo 2005, Fedriani and Boulay 2006, Smith and McWilliams
43 2014). Surprisingly, however, the extent to which plant traits and extrinsic factors affect interaction
44 frequency is unknown even for well-studied fruit-frugivore interactions (Jordano and Schupp 2000,
45 Saracco et al. 2005, Carlo and Morales 2008, Morales et al. 2013, Perea et al. 2013).

46 The relative contribution of plant intrinsic and extrinsic factors to variation in frugivore
47 strength among populations is difficult to assess since those two sorts of factors usually covary. For

48 example, for a given plant species fruit size and reward frequently vary among habitats or populations
49 due to differences in factors such as canopy cover, soil fertility, or temperature (e.g. Jordano 1995,
50 Parciak 2002, Fedriani 2005, Herrera 2009). Under such scenario of covariance, variation among
51 habitats or populations in interaction strength for a given frugivore guild cannot clearly be attributed
52 to either plant traits or extrinsic factors. Fortunately, field experiments based on the reciprocal
53 exchange and offer of ripe fruits among populations of a target plant species (i.e. 'reciprocal
54 translocation'; *sensu* Kawecki and Ebert 2004) represents a powerful, though neglected, approach to
55 address this issue (e.g. Alcántara et al. 2007). This approach consists in undertaking a number of local
56 fruit offering experiments, where traits (e.g. size and reward) of offered fruits vary widely due to both
57 intra and among population phenotype variation while extrinsic factors (e.g. abundance of different
58 frugivore guilds) are kept constant within each local experiment. Our approach could thus reveal the
59 relative importance of both sorts of factors in impinging variation among populations in fruit removal
60 rates by frugivores.

61 Functionally diverse vertebrate frugivores often vary among populations in density and activity
62 (e.g. Brodie et al. 2009, Fedriani and Delibes 2013, Peris et al. 2017). Furthermore, different frugivore
63 guilds are likely to exert different effects (e.g. seed dispersal vs. seed predation) and selection
64 pressures on the plant populations (Alcántara and Rey 2003, Fedriani and Delibes 2013). For instance,
65 some mammalian carnivores generally ingest whole fruits, transporting the seeds internally and
66 dispersing them away, acting thus as 'legitimate' seed dispersers (Traveset 1998). Large herbivores
67 such as ungulates usually ingest whole fruits though they grind all or most ingested seeds, acting
68 mainly as both fruit and seed predators (Perea et al. 2013). Some small mammals and birds may eat a
69 portion of the fruit' pulp without ingesting and dispersing the seeds (i.e. pulp feeders) though they do
70 enhance seed germination (Fedriani and Delibes 2013). Because different functional groups of
71 frugivores tend to differ in their relative abundances and foraging behaviors, and often have

contrasting effects on the plants they interact with, a full understanding of variation among population in frugivory strength requires a guild-specific approach.

This study identifies variation among tree populations in guild-specific frequency of fruit-frugivore interactions using for the first time a fruit 'reciprocal translocation' experiment. Our approach enabled multiple local offerings of highly phenotypically variable fruits, while the abundances of different frugivore guilds (as well as other extrinsic factors) were kept constant within each local experiment. To this end, we chose to study the interaction between *Pyrus bourgaeana* Decne (Rosaceae) and several frugivore guilds in Mediterranean Spain (Fedriani et al. 2012, 2018). The fruits of this small tree are consumed by a diverse coterie of frugivores, including seed dispersers (mainly medium size carnivores), pulp feeders (rabbits and small birds), and fruit predators (deer; Schaefer and Ruxton 2011). To disentangle the relative importance of extrinsic and intrinsic factors on the strength of plant-frugivore interactions, we performed reciprocal fruit translocation experiments in five localities during two consecutive fruiting seasons. Mammals are the most frequent consumers of *P. bourgaeana* fruits (Fedriani et al. 2012). Since they are scarcely limited in terms of fruit size and they show strong variations in their relative abundances among populations (Table 1), we expected that extrinsic factors (locality of fruit offering) would have a major effect on fruit removal rates as compared to intrinsic ones (fruit traits).

Methods

Study area and species

The study was carried out during November (i.e. the peak of fruit fall) of 2008 and 2009 in the Doñana National Park (37°9'N, 6°26'W; elevation 0-80 m), on the west bank of the Guadalquivir River estuary (SW Spain). The Doñana area comprises three main ecosystems: Mediterranean scrubland (where *P. bourgaeana* grows), mobile dunes, and marshes (Fig. 1). The climate is Mediterranean sub-humid,

characterized by dry, hot, long summers (June–September) and mild, wet winters (November–February; Żywiec et al. 2016).

Pyrus bourgaeana is a small (3–6 m height) deciduous tree endemic to the Iberian Peninsula (Spain, Portugal) and North Africa (Morocco) (Aldasoro et al. 1996). In the Doñana area, its distribution is very fragmented, with trees occurring at low densities (generally <1 individual ha⁻¹) in several Mediterranean scrubland patches that are isolated from each other by marshes, towns, or cultivations. In Doñana, each *P. bourgaeana* individual generally produces between 200 and 450 fruits per year. Fruits are non-dehiscent globose pomes (2–3 cm diameter) weighing ~6.7 g with a sugary water-rich pulp (Fedriani et al. 2012). Each fruit includes 1–5 viable seeds (46–91 mg each; Fedriani and Delibes 2009) with thin coats. When these fruits ripen, they drop to the ground from September to December and are harvested by the frugivore guilds discussed above (seed dispersers, fruit predators, pulp feeders, and seed-eating rodents; Fedriani and Delibes 2013). Seed dispersers are mostly medium sized mammalian carnivores such as badger (*Meles meles*) and red fox (*Vulpes vulpes*), although wild boars (*Sus scrofa*) also disperse some viable seeds (Fedriani and Delibes 2009, Fedriani et al. 2018). Pulp consumers such as rabbits (*Oryctolagus cuniculus*) and some birds usually eat to a variable extent the fleshy pulp, leaving the uneaten fruit parts with uneaten seeds under fruiting trees (Fedriani et al. 2012). Fruit predators such as red (*Cervus elaphus*) and fallow deer (*Dama dama*) ingest a significant fraction of whole fallen fruits, grinding all ingested seeds (Perea et al. 2013). Seed-eating rodents such as *Apodemus sylvaticus* and *Mus spretus* were not abundant in the study area, but they do prey on seeds mostly from fruits previously defleshed by rabbits (Authors, *unpublished data*). Despite its local sparseness, *P. bourgaeana* fruits represent an important resource for local vertebrate frugivores (Fedriani et al. 2012, Castro-Arenas 2012, Żywiec et al. 2016).

Study sites

To carry out the fruit 'reciprocal translocation' experiments, we selected five localities (3-15 km apart) within the Doñana area (called Reserva, Matagordas, Rocina, Hato Ratón, and Hinojos) where *P. bourgaeana* is relatively abundant (Fig. 1). Though they all are dominated by Mediterranean scrubland, they differ in densities of fleshy-fruited shrubs as well as in the presence and relative abundance of different frugivores (Table 1). Reserva is covered by scattered *Quercus suber* and *Pinus pinea* trees with dense Mediterranean scrubland dominated by *Halimium halimifolium*, *Rosmarinus officinalis* and *Stauracanthus* spp. Local density of fleshy-fruited shrubs, mostly *Phillyrea angustifolia*, is relatively low (Table 1). Matagordas is characterized by scattered *Q. suber*, *Olea europaea* var. *sylvestris*, *Fraxinus angustifolia*, and *P. pinea* with an understory dominated by *Pistacia lentiscus* growing singly or in small clumps separated by unvegetated sandy substrate or sparse *H. halimifolium*, *Stauracanthus* spp. and *Chamaerops humilis*. The density of fleshy-fruited shrubs (mostly *P. lentiscus* and *C. humilis*) is very high (Table 1). Rocina is a Mediterranean scrubland crossed by a stream and comprising scattered *P. pinea* with an understory of *Stauracanthus* spp., *Cytisus grandiflorus* and *H. halimifolium*. Local density of fleshy-fruited shrubs, mostly *Asparragus* spp., is low (Table 1). Hato Ratón has a vegetation similar to that in Matagordas (i.e. scattered *Q. suber* with understory dominated by *P. lentiscus*), but with a lower density of fleshy-fruited shrubs (Table 1). Hinojos vegetation is characterized by a *P. pinea* forest with understory of *P. lentiscus*, *C. humilis* and *H. halimifolium*. Density of fleshy-fruited shrubs (mostly *P. lentiscus* and *C. humilis*) is similar to that found in Hato Ratón (Table 1). Whereas Reserva, Matagordas and Rocina are within the National Park, where hunting is not allowed, Hato Ratón and Hinojos are located outside of the National Park, where hunting occurs (Fig. 1). This partially explains the generally higher frugivore abundances within the National Park.

Fruit characterization

To assess potential variation in fruit traits among the five *P. bourgaeana* populations, we measured fruit weight, number of seeds per fruit, seed weight, and the ratio pulp weight / seed weight both in 2008 (41 trees [4-12 per population], 189 fruits, 423 seeds) and 2009 (49 trees [7-15 per population], 223 fruits, 614 seeds). Most sampled trees (77.7%, n = 90) were the same individuals in both seasons and, within each population, were usually > 50m apart. Each season and for each tree we collected three to five representative ripe fruits that were taken to the lab and immediately characterized. Fruits aborted, infected by invertebrates, shriveled, or damaged in any way were not used (e.g. Fedriani and Delibes 2013). Also, all viable seeds were extracted, counted and weighted using a 0.001-g precision scale. The ratio pulp weight / seed weight was then estimated and used as an index of reward (e.g. Rey and Alcántara 2000).

Field experiments

We experimentally studied among population variations in the interaction strength (i.e. frequency) between *P. bourgaeana* fruits and different frugivore guilds. In each locality, to encompass environmental heterogeneity within each site without compromise the logistical viability of the experiments, we established two blocks >100 m apart and about 200m away from any fruiting pear tree (Fig. 1). Each block comprised 10 fruit-offering points (i.e. circular plots of 1m diameter) spaced ~10 m apart within a grid (3 rows and 4 columns). At each offering point, one ripe fruit from each target population was placed spaced about 20 cm in circular distribution (overall, five fruits) on the open ground (Fig. 1). Offered fruits were sampled one day before the experiments, using 10-15 trees from each target population and season (7-15 fruits per tree, depending on availability). Within each sampled tree, fruits representative in size were selected (i.e. those too small or too large were rejected). As above, fruits aborted, infected by invertebrates or shriveled were not used (e.g. Fedriani and Delibes 2013). Data from a previous study clearly support the idea that we able to select the

typical phenotype from each population, with mean size of offered well within the 95% confidence interval of the population (Fedriani and Delibes 2013, Authors *unpublished data*). To identify the offered fruits, they were marked on the pedicel with a small thread (not visible during the offerings) of a particular color for each population of origin. Previous studies indicated that frugivores usually harvest 1-3 fruits per visit (Fedriani and Delibes 2009, 2013); thus, five fruits was an adequate quantity to force frugivore choice. To facilitate the precise identification of frugivore visitors based on their footprints in the local sandy substrate, we cleaned carefully the offering point at the start of the experiment and then after each observation (e.g. Mendoza and Dirzo 2007, Fedriani and Delibes 2013, Peris et al. 2017). All offering points were checked early in the morning during five consecutive days and removed fruits were not replaced. To ensure that frugivores had simultaneously access to fruits from all five populations, in the analyses (below) we considered data concerning the first day of the fruit offering experiments. We classified visitors into three frugivore guilds as defined above: seed dispersers (badger, fox and wild boar), fruit predators (red and fallow deer), and pulp feeders (rabbit and small birds). Seed-eating rodents were very infrequent visitors and thus were not considered in our analyses.

Statistical Analyses

To estimate the relative importance of different levels on seed and fruit trait variation, we estimated the partitioning of total variation of particular fruit and seed traits among-localities, among-individuals, and within-individuals (residual) components using analyses of the variance components. All levels were considered as random effects, as required for variance partitioning. Analyses were conducted with the Proc Mixed SAS (SAS Institute, 2016). Then, variation among populations in fruit traits were analyzed by fitting generalized linear mixed models using the Proc Glimmix SAS (SAS Institute, 2016). For fruit weight, fruit reward to seed ratio, and seed weight normal error and identity link function was

used, whereas for seed number a Poisson error and log link function were specified. Because we tested for among-localities differences, population was considered as a fixed factor; however, season (2008 and 2009) and individual tree (nested within locality of origin) were included in the models as random factors (Bolker et al. 2009). For seed weight, fruit (nested within tree and locality of origin) was also specified as random factor.

The probability of visitation by different frugivore guilds (i.e. presence of frugivore tracks in the fruit offering points whether or not there was fruit removal) and the conditional probability of fruit removal (given that a frugivore guild has visited a fruit offering point) were also analyzed using the Proc Glimmix SAS (SAS Institute 2016). To model the probability of visitation by different frugivore guilds, each offering point was coded (1/0) depending on whether (1) or not (0) it was visited by a particular frugivore guild. In this analysis, we considered data concerning both the first day (see below) as well as accumulated visits during the five days of the experiments. Locality where fruits were offered (i.e. offering locality), frugivore guild and their second-order interaction were included in the model as fixed factors.

The probability of fruit removal (1/0) was modeled as a function of offering locality, fruit origin, frugivore guild, as well as the second-order interactions between fruit origin and frugivore guild and between fruit origin and offering locality. In a preliminary analysis, the second order interaction between offering locality and frugivore guild was also included in the model but this more complex model did not converge; thus, variations in the frequency of removal by different guilds in each offering locality were examined by chi-square analyses of contingency tables. Because of the binomial nature of response variables (i.e. frugivore visitation [1/0], fruit removal [1/0]), binomial error and logit link function were specified. In both models (frugivore visitation, fruit removal), season (2008 and 2009), block (nested within offering locality) and offering point (nested within block and offering locality) were included as random factors (Bolker et al. 2009). Similar hierarchical nested designs are commonly use in the ecological literature (e.g. Dalling et al 1998, Herrera et al. 2002, Parra-Tabla et al.

2009, Fedriani and Delibes 2013). When the interaction between any two factors was significant, we performed tests for the effect of a given factor at the different levels of the other factor using the SLICE option in the LSMEANS statement of the Proc Mixed SAS (SAS Institute, 2016). Low frugivore visits or fruit removal in Hinojos and Rocina prevented us from including data from these localities in some analyses. In those cases, we examined differences within these localities by means of chi-square analyses of contingency tables using SAS PROC FREQ (SAS Institute, 2016). To maximize our accuracy in the identification of vertebrate frugivores when analyzing fruit removal, we considered only offering points visited by a single frugivore guild (e.g. Fedriani and Delibes 2013). Also, to ensure that fruits from all localities were simultaneously available for frugivores, only data concerning the first experimental day were used in this analysis.

Results

Sources of variation in fruit and seed traits

For seed weight, variance within trees (i.e. among fruits) explained 43.3% and 75.1% of the total variance in 2008 and 2009, respectively. Among-localities and among-individuals variation accounted for up to 16.5% and 45.7%, respectively, of the total seed trait variance. Data on fruit traits indicated that most of the variance was explained by differences among individuals (40.8-66.8% of total variance). Among-localities and within individual (i.e. among fruits) variation accounted for up to 33.9% and 25.2% of the total fruit trait variance, respectively. Thus, although most variance occurred at the individual level, there was also substantial variation in fruit and seed traits among populations.

Considering samples from the five populations together, fruit weight was very variable with a coefficient of variation of 60% (mean $\pm$ 1SE = 10.08 $\pm$ 6.09 g, n = 412, range = 1.21 – 53.76 g). Our mixed model for fruit weight revealed that, despite marked variation among and within individual trees (see above), there were strong and significant differences among localities ($F_{4,50} = 8.83$, $P < 0.0001$).

Specifically, mean fruit weight in Reserva was 2.1-fold heavier than in Hato Ratón, Matasgordas and Hinojos, and 1.5-fold heavier than in Rocina (Fig. 2a). Fruit reward to seed ratio showed the greatest variation among all fruit traits (45.70 ± 41.38 , $n = 391$, range = 6.56 – 302.03, CV = 91%). Fruit reward to seed ratio also differed significantly across localities ($F_{4,50} = 4.27$, $P < 0.01$). Specifically, the mean reward to seed ratio in Reserva was 2.2-fold greater than in Hato Ratón, Matasgordas and Hinojos, and 1.6 greater than in Rocina (Fig. 2b). Seed number also showed a high overall variation (2.45 ± 1.62 , $n = 423$, range = 0 – 9, CV = 66%). There were significant differences among populations in seed number ($F_{4,51} = 2.87$, $P < 0.05$). Matasgordas, Hinojos and Hato Ratón were the populations with greatest seed number per fruit (Fig. 2c). Finally, overall variation in seed weight was the lowest of all fruit traits considered (0.09 ± 0.04 g, $n = 1037$, range = 0.01 – 0.85 g, CV = 51%). Nonetheless, there were significant differences in mean seed weight among populations ($F_{4,51} = 7.01$, $P < 0.0001$), with seeds from Reserva, Rocina, and Hinojos being heavier than those from Matasgordas and Hato Ratón (Fig. 2d).

Frugivore visits

During the first day of the experiment, 66.5% (133 of 200) of the offering points were visited. Most visits (106 of 133) were by a single frugivore guild, whereas only 20.3% of visits (27 of 133) were by two or up to three guilds. Our mixed model for the first day visitation data revealed that frugivore guilds significantly differed in their probability of visit ($P < 0.0001$, Table 1a). In particular, the overall probability of visit by pulp feeders was over 3.6-fold greater than for both seed dispersers and fruit predators (Fig. 3a). Offering locality did not have an effect as a main factor ($P = 0.114$, Table 1a); however, the significant interaction between offering locality and frugivore guild ($P < 0.0001$, Table 1a) indicated that the probability of visit by each guild was inconsistent among study sites (Fig. 3a). For instance, whereas pulp feeders were the most likely visitors in Hato Ratón, Matasgordas, and Rocina

(tests of slices, $F_{2,445} > 4.23$, $P < 0.05$), no differences among guilds in the probability of visit were found in Reserva (test of slices, $F_{2,445} = 0.45$, $P = 0.639$). In Hinojos (that was excluded from the model), the frequency of visit did not show differences among pulp feeders and seed dispersers ($\chi^2 = 2.16$, d.f. = 1, $P = 0.14$; Fig. 3a) whereas fruit predators were absent.

When considering the accumulated visits throughout the five days of experiment, results were consistent with those reported above. For example, frugivore guilds strongly differed in their probability of visit ($P < 0.0001$, Table 1a), with pulp feeders being 2.1 and 1.7-fold more frequent visitors than seed dispersers and fruit predators, respectively (Fig. 3b). Also, the strongly significant interaction between offering locality and frugivore guild ($P < 0.0001$, Table 1a) indicated that the probability of visit by the three frugivores guilds differed among study sites (Fig. 3b). Whereas pulp feeders were the most frequent visitors at Hato Ratón, Matasgordas and Rocina (test of slices, $F_{2,445} > 8.99$, $P < 0.0001$; Fig. 3b), in Reserva seed dispersers were the most frequent visitors (test of slices, $F_{2,445} = 4.46$, $P = 0.012$). Nonetheless, unlike the results for the first day of experiment, the frequency of visits by pulp feeders in Hinojos more than doubled that found for seed dispersers ($\chi^2 = 16.2$, d.f. = 1, $P < 0.0001$; Fig. 3b).

We found a significant positive relationship between frequency of visits by pulp feeders and the density of alternative fleshy-fruited plants across populations and the two sampled years (Spearman correlation, $r_s = 0.728$, $n = 10$, $P = 0.017$). Significant relationship between frequency of visits and the density of alternative fleshy-fruited plants was found neither for seed disperser nor fruit predators ($P > 0.187$).

Fruit removal

Overall, frugivores removed about one third (31.1%) of offered fruits (i.e. 165 of 530). The mean number ($\pm 1SE$) of fruits removed per visit was 1.21 ± 0.18 , 1.89 ± 0.56 , and 2.61 ± 0.50 for pulp feeders, fruit predators, and seed dispersers, respectively. When we considered all offering points, pulp feeders

removed fruits (52.1%, $n = 165$), whereas seed dispersers (28.5%, $n = 165$) and fruit predators (19.4%, $n = 165$) removed lower and similar amounts of fruits.

Unexpectedly based on marked variation among localities in fruit size and reward to seed ratio, removal of fruits from different localities were rather similar ($P = 0.404$), being highest for Matasgordas and Hinojos (0.52 ± 0.14 and 0.51 ± 0.14 , respectively), intermediate for Hinojos and Rocina (0.40 ± 0.13 and 0.41 ± 0.13), and lowest for Reserva (0.32 ± 0.12). Furthermore, the interaction between fruit origin and frugivore guild was not significant ($P = 0.930$; Table 1b), indicating that no frugivore guild selected fruits from any locality. As predicted, the per visit probability of fruit removal varied significantly across frugivore guilds ($P < 0.001$, Table 1b). For instance, given that an offering point was visited by a particular frugivore guild, the per visit probability of removal for both fruit predators (0.55 ± 0.13) and seed dispersers (0.50 ± 0.13) doubled that found for pulp feeders (0.26 ± 0.12).

Unexpectedly, offering locality (excluding data from Rocina) had no significant effect as a main factor ($P = 0.858$, Fig. 4a). Though the interaction between guild and offering locality could not be included in the model, the proportion of removed fruits by different guilds strongly varied among localities ($\chi^2 = 122.13$, d.f. = 8, $P < 0.0001$, Fig. 4b). For instance, fruit removal by seed dispersers was 5.6 and 1.6-folds greater in Reserva than in Rocina and Hinojos, respectively, whereas they did not remove any fruit in Hato Ratón and Matasgordas (Fig. 4b). Fruit removal by fruit predators was 4.0-fold greater in Reserva than in Matasgordas, whereas they did not remove any fruit in Hato Ratón, Rocina and Hinojos (Fig. 4b). Pulp feeders removed fruits from all localities except in Rocina, being fruit removal 8.5, 2.3 and 1.5-folds greater in Hato Ratón than in Reserva, Hinojos, and Matasgordas, respectively (Fig. 4b),

There was no relationship between fruit removal by pulp feeders, seed dispersers, or fruit predators and the density of alternative fleshy-fruited plants across populations during the two sampled years ($P > 0.163$).

Discussion

Quantifying variations among populations in fruit-frugivore interaction strength is critical for a full understanding of these ecologically-relevant relationships (Levey et al. 2002, Dennis et al. 2007, Schaefer and Ruxton 2011, Fleming and Kress 2013). Our reciprocal translocation of *P. bourgaeana* ripe fruits revealed that, even though overall fruit removal strength was similar among most localities (e.g. García et al. 2014), there were marked variations among populations in the strength of guild-specific fruit-frugivore interactions. Because the three frugivore guilds considered (seed dispersers, fruit predators, and pulp feeders) play contrasting roles in *P. bourgaeana* dynamics (Fedriani and Delibes 2013, Fedriani et al. 2018), our study supports the idea that each tree population might experience a rather unique combination of demography effects (seed dispersal, pulp removal, seed predation). It also highlights the importance of accounting for functional diversity in frugivore guilds when estimating spatial variations in seed dispersal strength (i.e. fruit removal does not necessary equal to seed dispersal).

High variation in fruit traits and lack of frugivore selection

Selection of phenotypically variable fruits often triggers frugivore selection pressures on fruit traits (Sallabanks 1993, Wheelwright 1993, Jordano 1995, Galetti et al. 2013). Sallabanks (1993) and Wheelwright (1993) showed that birds selected fruiting plants with greater than average fruit size. Conversely, Jordano (1995) and Alcántara and Rey (2003) in southern Spain found that small birds selected fruits with small seeds (of *Prunus mahaleb* and *Olea europaea*, respectively) because gape size prevented the ingestion of larger fruits. Though, as expected, *P. bourgaeana* fruit traits markedly varied among tree populations we found no evidence of fruit selection by any frugivore guild. One possibility explaining this result is that different frugivore guilds selected fruits based on contrasting trait sets given their different fruit processing strategies that (e.g. Levey 1987, Sallabanks 1993). For example, lack of selection of fruit reward (i.e. pulp amount) could be expected in the case of fruit predators (i.e. deer) since these large herbivores probably obtain nutrients from both the pulp and also the seed itself. Other possibility to be considered in future studies is variation among focal *P.*

bourgaeana populations being based on fruit traits other than size or reward (e.g. volatile compounds, chemical defenses; Lomáscolo et al. 2010, Schaefer and Ruxton 2011, Whitehead et al. 2016, Peris et al. 2017).

Extrinsic factors and guild-specific variation in frugivory strength

Variations among habitats in the strength of fruit-frugivore interactions are pervasive in tropical, temperate, and Mediterranean habitats (e.g. Carlo et al. 2003, Hampe et al. 2008, Carlo and Yang 2011, Perea et al. 2013). These variations often relate to changes in the local abundance of frugivores which, in turn, correlate with environmental factors (e.g. habitat, human disturbances; Herrera 1998, Fuentes et al. 2001, Perea et al. 2013). In our Mediterranean ecosystem, the higher abundance of seed dispersers (particularly foxes) in Reserva as compared to Hinojos and Hato Ratón is likely related to the higher protection and lack of hunting activity in Reserva. Lack of hunting in Reserva and Matasgordas also explain the higher abundance of fruit predators (deer) as compared to Hinojos and Hato Ratón. On the other hand, higher abundance of pulp feeders (mostly rabbits) in Matasgordas and Hato Ratón is likely related to a lower local incidence of rabbit diseases (Fedriani et al. 1998, Moreno et al. 2008).

Variation among the five *P. bourgaeana* populations in guild-specific fruit removal rates (related to changes in their relative abundances) have probably important effects on the local tree dynamics. For instance, seed dispersers (foxes and badgers) were most active in Reserva (Fig. 3b), which may be responsible of the observed tree colonization of vacant habitats in this area (Fedriani et al. 2017; Authors *unpublished data*). Such population expansion is taking place even though seed predators (red and fallow deer) are also abundant in Reserva, where every season they depredate large fractions of *P. bourgaeana* crops (Fig. 4b; Fedriani and Delibes 2013). Pulp feeders (mostly rabbits) were particularly active in Hato Ratón, Hinojos and Matasgordas. By defleshing *P. bourgaeana* fruit, they enhance

seedling emergence and establishment (Fedriani et al. 2012) also affecting the tree dynamics in a contrasting manner across studied localities. Other extrinsic factors could have also contributed to variation among populations in guild-specific fruit removal strengths. For example, though there was not general relationship between frugivory strength and availability of alternative fruits, the highest density of fleshy fruits in Matasgordas (Fedriani and Delibes 2013, Authors *unpublished data*) may have led the locally abundant frugivores to focus their foraging on fruits from species other than *P. bourgaeana*. This could explain the relative low fruit removal rates in Matasgordas (where *C. humilis* and *P. lentiscus* are very abundant). Also, fruit removal in Rocina was almost null, even though the three frugivore guilds frequently visited our fruit offering points in this locality (Fig. 2). The presence in Rocina of highly preferred fleshy-fruited species (e.g. *Arbutus unedo*) could partially explain such an intriguing result, though further research is certainly needed to address this question. On the other hand, since the more a frugivore's attention is directed towards potential predators the less effort it invests in fruit foraging (Howe 1979, Fedriani and Boulay 2006), variation in predation risk among populations could lead to differences in fruit removal strengths. This could be the case of the red fox, which rarely visited our fruit offering points in Matasgordas, precisely where its intraguild predator, the Iberian lynx (*Lynx pardinus*), is most abundant (Fedriani et al. 1999). The differences among sites in environmental factors seemed to lead to variation in the abundance of different frugivores guilds which in turn resulted in different demography effects among *P. bourgaeana* populations.

Concluding remarks

Since mammals were the main *P. bourgaeana* dispersers (see Fedriani and Delibes 2009) our data seem to support the existence of a “generalized mammalian syndrome” (Herrera 1989, Lomáscolo et al. 2008, Lomáscolo et al. 2010). However, a tight adaptation between this tree and its dispersers is unlikely due to several reasons. Firstly, as we revealed here, local factors extrinsic to *P. bourgaeana*

appear to impinge more strongly than fruit traits on the strength of these plant-frugivore interactions, constraining the potential for adaptation between the tree and its frugivores. Secondly, a large fraction of fruit and seed trait variation took place within individual trees, which often limits the ability of frugivores to exert phenotypic selection (Herrera 2009). Thirdly, seed dispersers (foxes, badgers) and fruit predators (deer) often exert conflicting pressures on plant traits (Fedriani and Delibes 2013) that can cancel each other (e.g. Alcántara and Rey 2003, Fedriani et al. 2004, Siepielski and Benkman 2010). Finally, *P. bourgaeana* currently experiences an environment very different from the one under which it evolved in the western Mediterranean basin (e.g. Guimarães et al. 2008). For instance, from the Pleistocene until a few decades ago, probable seed dispersers such as the Barbary macaque (*Macaca sylvanus*), the brown bear (*Ursus arctos*), and the wolf (*Canis lupus*) have become extinct in the Doñana area (Fedriani and Delibes 2009).

Though fruit removal rates were similar among most tree populations, the importance of different guild consumers varied markedly. Such variations in the incidence of different frugivore guilds led to variable effects on tree dynamics across populations, highlighting the value of accounting for functional diversity when estimating spatial variations in seed dispersal strength. Our approach allows undertaking a considerable number of local fruit offering experiments, where traits of offered fruits vary widely while extrinsic factors are kept constant within each local experiment. This approach facilitates investigations of the relative importance of extrinsic factors and fruit trait in mediating interactions in other similar systems (see reviews in Levey et al. 2002 and Dennis et al. 2007) as well as in other sorts of interactions comprising plants dispersed by rodents (e.g. Beck and Vander Wall 2010), myrmecochory (e.g. Alcántara et al. 2007), and diplochorous systems (*sensu* Vander Wall and Longland 2004).

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Table 1: Density of fleshy-fruited plants and relative abundances of different frugivore guilds at the five studied localities within the Doñana area, Southwestern Spain.

Locality	Density of fleshy fruited plants [†]	<i>P. bourgaeana</i> density [†]	Disperser abundance	Pulp feeder abundance	Fruit predator abundance	Reference
Reserva	200.0±1.79	0.089±0.054	High	Low	High	1-4,7
Matasgordas	1856.7±7.59	3.096±0.396	Intermediate	Very high	High	4-6,7
Rocina	93.3±1.15	0.195±0.066	Low	Low	Intermediate	7,8
Hato Ratón	693.33±3.40	1.344±0.470	Low	High	Low	7,8
Hinojos	633.33±3.72	2.292±0.318	Low	Low	Low	7,8

[†] ind·ha⁻¹ (mean±1SE); References: ¹Rau 1987, ²Revilla and Palomares 2002, ³Moreno et al. 2008, ⁴Braza et al. 1984, ⁵Fedriani et al. 1999, ⁶Palomares et al. 2001, ⁷Authors *unpublished data*, ⁸Data from Natural Processes Monitoring Group (Doñana Biological Station).

Table 2: Main results from generalized linear mixed models evaluating the effect of (a) fruit offering locality and frugivore guild on the probability of visitation based on data from either the first day or the whole experiment, and (b) fruit offering locality, fruit origin, and frugivore guild on the conditional probability of fruit removal based on data from the first experimental day (when fruits from all origins were present). Note that a preliminary model including the third-order interaction did not converge.

(a) Visits	First day			Whole experiment		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Offering locality (<i>OL</i>)	3, 4	3.82	0.1139	3, 4	5.92	0.0593
Guild (<i>G</i>)	2, 463	27.17	<0.0001	2, 463	22.73	<0.0001
<i>OL</i> * <i>G</i>	6, 463	5.00	<0.0001	6, 463	9.02	<0.0001

(b)	Removal [†]		
	d.f.	<i>F</i>	<i>P</i>
Offering locality (<i>OL</i>)	3, 4	0.25	0.8578
Origin (<i>O</i>)	4, 392	1.01	0.4039
Guild (<i>G</i>)	2, 392	7.35	0.0007
<i>O</i> * <i>G</i>	8, 392	0.38	0.9298
<i>O</i> * <i>OL</i>	12, 392	0.62	0.8247

[†]A model including the third-order interaction *OL***O***G* did not converge.

Figure legends:

Fig. 1: Diagram of the experimental design at different scales. (a) Sketch map of the Doñana National Park showing the location of the five studied *Pyrus bourgaeana* populations and the main habitat types. Limits of the National and the Natural parks are shown by continuous dashed lines, respectively; (b) pair of blocks (>100 m apart), each one comprising ten fruit offering points; and (c) offering point comprising five fruits (one per locality of origin).

Fig. 2. Model corrected mean ($\pm 1SE$) of (a) fruit weight, (b) fruit reward to seed ratio, (c) seed number per fruit and (D) seed weight at five *Pyrus bourgaeana* populations of south-western Spain. For each population, different lowercase letters denote significant ($P < 0.05$) differences.

Fig. 3. Model corrected mean ($\pm 1SE$) likelihood of visit to *Pyrus bourgaeana* fruit offerings points by three frugivore guilds (seed dispersers, fruit predators and pulp feeders) during (a) first day and (b) whole field experiments at five localities of south-western Spain. Significant differences among guilds are indicated for each locality (* = $P < 0.05$, *** = $P < 0.001$, N.S. = non-significant). For Hinojos, the observed proportions of visits and the significance level obtained by chi-square analysis are shown.

Fig. 4. Graphical representation of model corrected mean ($\pm 1SE$) of *Pyrus bourgaeana* fruit removal likelihood at five localities of south-western Spain by (a) different frugivore guilds and (b) fruit offering locality. (c) Observed proportion of removed fruits by different frugivore guilds at each offering localities. In (b) for Rocina the observed proportion of removed fruits is shown.

Figure 1:

Fig. 2

Fig. 3

Fig. 4