



## Research article

# Effects of habitat fragmentation on frugivorous birds and on seed removal from *Pistacia lentiscus* in two contrasting fruiting seasons

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## ABSTRACT

Successful animal seed dispersal is the result of the interaction between frugivore behavior and the distribution of food resources, which can vary over space and time. We evaluated the interaction between avian frugivores and the masting shrub *Pistacia lentiscus* in both connected and isolated forest fragments along the Guadalquivir valley (south Iberian Peninsula) in two contrasting fruiting seasons (mast and non-mast). We compared the abundance and composition of avian dispersers and seed predators, recorded fruit removal rates by dispersers and predators, and investigated potential changes in the arrival of seeds to forest fragments. Our results showed that there was a greater abundance of dispersers in connected than in isolated fragments in the mast season (*i.e.* high fruit availability) but the opposite pattern in the non-mast season (*i.e.* low fruit availability). The effects of habitat fragmentation were more noticeable on medium-sized than small bird dispersers. Medium-sized birds were more abundant in isolated forest fragments but their abundance was highly dependent on the season, while small bird dispersers were apparently unaffected by fragmentation. Seed removal rates were higher in isolated than in connected fragments in the mast season but not in the non-mast season; predation rates were negligible in both seasons. Seed arrival was consistent between seasons and microhabitat where the dispersed seeds were deposited, most seeds being dispersed under the canopy of female *Pistacia* plants. We highlight the influence of the interplay between seasonality and landscape configuration on patterns of frugivore-mediated seed dispersal. Thus, despite its direct link to plant–frugivore interaction, the effects of habitat fragmentation on frugivores and plants were decoupled in our study system. These decoupled responses seemed to be chiefly due to the high feeding dependence of dispersers on *P. lentiscus* fruits.

## 1. Introduction

Seed dispersal is a key step in the life cycle of plants as it provides an independent dispersal phase for a new and genetically distinctive individual that can potentially colonize and establish itself in novel environments (Jordano, 2017). Consequently, seed dispersal is a determinant factor in the structure and dynamics of plant populations and communities (Janzen, 1970). In animal seed-dispersed plants, frugivores either regurgitate or defecate undamaged seeds away from parent plants (Jordano, 2000). The probability of seed removal and the patterns of seed dispersal are thus strongly influenced by spatial environmental factors affecting frugivore abundance and behavior such as food availability, the heterogeneity of microhabitat in terms of shelter and

breeding sites, and the functional connectivity between habitats (Corrêa Côrtes and Uriarte, 2012). However, current changes in landscape configuration due to human activities leading to forest loss and fragmentation may alter the abundance of both fruiting plants and frugivores (Stiles, 1980; Restrepo and Gomez, 1998; Restrepo et al., 1999).

Habitat loss and fragmentation change the original spatial structure of the landscape by reducing the size and connectivity of remaining habitat fragments, which will probably affect the mutualistic interactions of animal seed dispersal (Emer et al., 2018). One key aspect to consider when assessing the effects of fragmentation on plant–animal seed dispersal is the relative mobility of the seed disperser. For example, habitat fragmentation can alter the distribution of certain

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frugivorous species with low mobility that are restricted to specific environments, while other frugivores with greater mobility may be capable of using a non-forested matrix and thus be able to increase their abundance in moderately marginalized fragmented habitats (Farwig et al., 2006). Furthermore, habitat fragmentation may change the composition of the disperser guild by reducing the abundance of large-bodied avian dispersers, thereby decreasing the probability that long-distance dispersal events from small habitat fragments will take place (Uriarte et al., 2011). Generally, large frugivores will have stricter feeding and habitat requirements than smaller ones, which are able to live in small and low-quality forest fragments (Uriarte et al., 2011).

However, not all frugivorous birds establish mutualistic interactions and disperse seeds. Some species act as antagonists since they eat the seeds (e.g. granivorous birds) and kill the embryo, thereby reducing female plant fitness (Verdú and García-Fayos, 2001). Habitat fragmentation may also affect seed removal by modifying the behavior of animal dispersers (Herrera, 1995), thereby altering the balance between mutualistic and antagonistic interactions (Jules and Rathcke, 1999; Herrera et al., 2011). A shift toward more antagonistic interactions (e.g. seed predation) and less seed removal will harm forest regeneration dynamics (Neuschulz et al., 2016). At the end of the fruiting period the plant will have interacted with both dispersers and predators and the relative balance between them will determine the net amount of seed dispersal. In the long term, habitat fragmentation may change the regenerative potential of plant species by affecting the recruitment and regeneration of plant populations (García et al., 2012; Rey and Alcántara, 2013).

Additionally, seed dispersal mediated by animal vectors is strongly influenced by seasonal variation in fruit production. This is the case of masting behavior (i.e. the annual variation in fruit production) in certain plant species that represent key fruit resources for frugivorous birds. Similarly, masting can reduce seed predation by satiating predators through an abundance of available fruit and, consequently, may improve plant fitness (Mezquida and Olano, 2013). Masting can affect the presence and abundance of frugivorous birds in forests and therefore plant–frugivore interactions (Jordano, 1985). Movements by frugivorous animals may in fact reflect the underlying seasonal variability in the availability of fruit resources rather than the nature of the habitat cover itself (Lehouck et al., 2009; Herrera and García, 2010; Herrera et al., 2011). Despite the importance of seasonal variation imposed by masting, to date only a few studies spanning a temporal window of more than a single season have ever been published (e.g. Jordano, 1987; Alcántara et al., 1997; Herrera and García, 2009; Herrera et al., 2011).

Seed removal by animals is also affected by spatial variation in microhabitat heterogeneity. This process frequently exhibits non-random patterns biased toward certain microhabitats within the landscape (Schupp et al., 2002). Consequently, frugivores may disperse seeds unevenly by occupying preferred microhabitats, which will create contagious spatial distributions of dispersed seeds (Schupp et al., 2002). Ultimately, a nucleation process of this nature affects seed survival and seedling establishment, as well, subsequently, as the structure and dynamics of plant populations and communities (Howe and Smallwood, 1982; Wang and Smith, 2002; Nathan, 2006; Clark et al., 2007; González-Castro et al., 2015).

In this study, we evaluated the effects of habitat fragmentation on the seed dispersers and seed predators of the Mediterranean masting species *Pistacia lentiscus* L. (Anacardiaceae) in two contrasting fruiting seasons (high and low production). More specifically, we (i) compared the abundance and composition of the avian frugivores, (ii) recorded fruit-removal rates by fruit dispersers and predators, and (iii) investigated potential changes in the final destination of seeds. We expected to find greater frugivore richness and abundance in connected than in physically isolated forest fragments. In addition, we expected small-sized frugivorous bird species to dominate in the frugivore guild in connected forest fragments, but that medium-sized birds would occur in both isolated and connected forest fragments (Uriarte et al., 2011).

Furthermore, since *P. lentiscus* is a masting species, we hypothesized that there would be greater dispersal and predation rates during a high fruit production season (the mast season, hereafter), and that interactions would be similar in both connected and isolated forest fragments during the mast season. Finally, because frugivorous birds visit female plants for longer and regurgitate or defecate the seeds in the same place as they ingest them, we expected higher levels of seed dispersal under female *Pistacia* plants than in other microhabitat types (Verdú and García-Fayos, 2002; González-Varo et al., 2018).

## 2. Material and methods

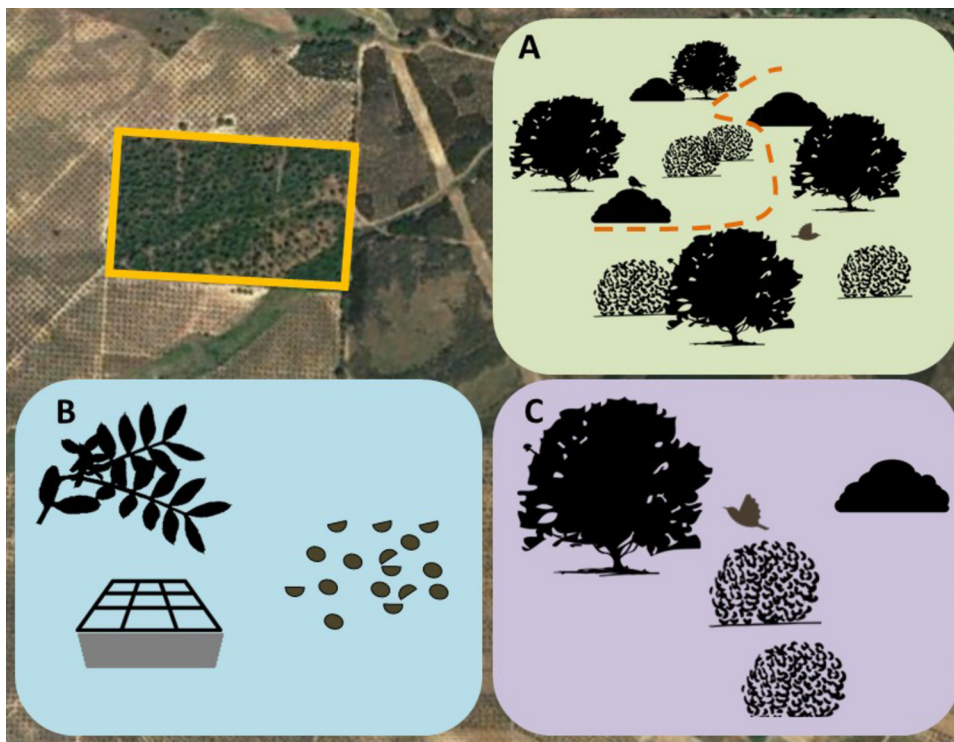
### 2.1. Study species

*Pistacia lentiscus* is a common evergreen sclerophyllous shrub of up to 3–5 m in height, widely distributed throughout the Mediterranean region. It is dioecious and wind-pollinated; its fruit consist of one-seeded drupes that ripen in September–March (Verdú and García-Fayos, 1998). Fruit ripening is associated with a change of color from white to red and then to black. Black fruits are most likely to bear a viable seed, while red and white fruits are either deceptive fruits of parthenocarpic origin or have aborted embryos (Jordano, 1989; Albaladejo et al., 2009, 2012). Masting is a common trait in the genus *Pistacia* (Lyles et al., 2009); however, the high temporal variability in *P. lentiscus* fruit production implies a similar irregularity in food availability for frugivorous birds (Herrera et al., 1998). The production of deceptive fruits has been associated with less seed predation by granivorous birds (Verdú and García-Fayos, 2001). Seed predator birds break the hard endocarp of the fruit, discard the two valves, and eat the seed inside. On the other hand, seed disperser birds eat only the fleshy pericarp of the fruit and defecate or regurgitate the seed intact within the hard endocarp. Classical census studies and recent DNA barcoding techniques applied to bird droppings have revealed that four bird species are the main seed dispersers (legitimate dispersers) of *P. lentiscus* in our study region: two warbler species (*Sylvia melanocephala* and *Sylvia atricapilla*), the European robin (*Erithacus rubecula*), and the common blackbird (*Turdus merula*) (Jordano, 1989; González-Varo et al., 2014; Parejo-Farnés et al., 2018). *P. lentiscus* is regarded as a keystone species in Mediterranean forests and plays an important role in ecosystem processes and services (Parejo-Farnés et al., 2017).

### 2.2. Study area

This study was conducted in the Guadalquivir River valley (S Iberian Peninsula), where there is a long history of human land management whose legacy is a landscape of vast intensively cultivated and deforested areas (Aparicio, 2008). To conduct this study, we selected four forest fragments in the region (Fig. 1) categorized either as “connected” or “isolated”, following the integral index of connectivity (IIC) used in Conefor 2.6 (Saura and Torné, 2009). We used this index to measure the fragment connectivity and flow of each forest fragment relative to other fragments in the region containing populations of *P. lentiscus*. The parameter IIC can be partitioned into two distinct fractions: IIC<sub>intra</sub>, which is the contribution of a given fragment *i* in terms of its intra-fragment connectivity, IIC<sub>flux</sub>, which is the area-weighted dispersal flux through the connections of a fragment *k* to or from all of the other fragments in the landscape (where *k* is either the start or end fragment of the connection between fragments). The physical characteristics and connectivity metrics for each fragment are shown in Table S1. Forest fragments HNJ and CHN are sizeable (> 10 ha) and are connected to other forest fragments with large populations of *P. lentiscus*. On the other hand, forest fragments VIS and CRB are small (< 10 ha) and are physically isolated and have extremely low values of connectivity with conspecific populations of *P. lentiscus* in a 5 km radius in the surrounding landscape (Table S1).

Although other fleshy-fruit species are available in the study



**Fig. 1.** Schematic representation of the sampling design carried out in each forest fragment in two consecutive seasons. A: Recording of frugivorous and predator abundance along dynamic transects. B: Tracking across the fruiting season of seed removal and predation rates using censuses and seed traps. C: Monitoring spatial patterns in seed deposition using seed traps in different microhabitats within the forest fragments (see text for details).

fragments (e.g. *Myrtus communis* L., *Olea europaea* L., *Phillyrea angustifolia* L., and *Crataegus monogyna* Jacq.), *P. lentiscus* is the most important fruit resource because of its abundance and the high lipid content of its fruit (Herrera, 1984, 1995).

### 2.3. Initial fruit availability

The study was conducted in two consecutive seasons (2012–13 and 2013–14) with contrasting scenarios of fruit abundance in the forest fragments: the first season was a mast year for *P. lentiscus*, while the second was a non-mast year. In order to quantify the initial fruit availability for avian frugivores we first estimated fruit density within the canopy (fruit  $m^{-2}$ ) at the beginning of the dispersal season (September) for each selected plant (10 per forest fragment). We counted the total number of fruit within 10  $15 \times 15$  cm quadrats randomly placed throughout the plant canopy (0.225  $m^2$  per sampled plant) and to calculate total individual fruit production extrapolated the value to the whole individual surface. We calculated plant individual surfaces as the surface of a half ellipsoid of revolution by measuring major and minor axes of the vertical projection of the canopy.

### 2.4. Abundance of seed dispersers and predators

Censuses were performed in the two study seasons from the beginning of fruit ripening (September) until fruit depletion (April). In each of the study fragments, we recorded bird abundance along 300-m transects (two per forest fragment) twice a day, between 09.00 and 12.00, every 3–4 weeks (Fig. 1). Frugivorous birds were identified by sound and sight (e.g. Seoane et al., 2006; González-Varo, 2010). We classified each individual bird species according to its behavior as belonging either to the seed disperser or seed predator guild (Herrera, 1984; Jordano, 1987; González-Varo, 2010); within the disperser guild, we also differentiated between small-sized birds (e.g. *Sylvia* spp.) and medium-sized birds (e.g. *Turdus* spp.).

### 2.5. Seed removal and predation rates

To determine seed removal and predation rates of *P. lentiscus* fruit over fruiting seasons, we selected 10 female shrubs in each forest fragment. We marked four branches on each shrub and monitored the ripening of their fruit and their disappearance due to either predation or dispersal. We monitored these shrubs every 3–4 weeks, completing a total of five monthly observations in each sampling season. In each survey, all the studied fragments were visited during the same week. We considered the fruit that disappeared from a branch between two consecutive observations as having been removed by legitimate dispersers. We assumed that the fraction of fruit that remained on tagged branches were undispersed (Alcántara et al., 1997; Jordano and Schupp, 2000). To correct dispersal rates with fallen and predated fruit we placed seed collectors above the ground, below the canopy of the selected plants. These collectors consisted of  $31 \times 20$  cm aluminum trays covered with a wire mesh of 5 mm that prevented post-dispersal seed predation by rodents. Every two valves in the collecting trays were counted as one predated fruit.

We estimated the total proportion of fallen fruit for each plant  $i$  ( $F_i$ ) by dividing the number of fallen and predated fruit (collected in the above-ground trays) by the density of fruit in the entire canopy of the plant (see González-Varo (2010) for a similar procedure). The dispersal rate (proportion of fruits consumed by dispersers) was indirectly calculated as  $D'_i = D_i \times (1 - F_i)$ , where  $D_i$  is the number of missing fruit from the branches between two consecutive observations and  $F_i$  is the number of non-dispersed (fallen and predated) fruits. The dispersal rate was calculated for each observation and the number of fruit in the canopy was corrected by subtracting the number of fallen and dispersed fruit in the previous observation from the original number of fruit in the canopy. The predation rate was calculated directly from the number of endocarp valves found in the collectors below each selected plant.

### 2.6. Seed rain across microhabitats and years

To determine the spatial and temporal pattern of dispersed seeds within each of the four study fragments and over the two study seasons,



**Table 1**

Results of the generalized linear models (GLMs) and mixed model (GLMM) testing the effects of fragment type, fragment identity (nested within type) and temporal variables (season and/or month) on the response variables initial fruit availability, abundance of seed dispersers and predators, and seed dispersal rates. Significant terms are highlighted in bold.

Source of variation	$\chi^2$	df	P-value
<b>Initial fruit availability</b>			
Type	2.467	1	0.113
Fragment (within type)	17.716	2	< 0.001
Season	21.153	1	< 0.001
Type $\times$ season	0.161	1	0.686
<b>Total seeds dispersers</b>			
Type	5.086	1	0.024
Fragment (within type)	0.836	2	0.658
Season	6.162	1	0.013
Type $\times$ season	7.830	1	0.005
<b>Small-sized dispersers</b>			
Type	1.631	1	0.201
Fragment (within type)	2.073	2	0.354
Season	4.377	1	0.036
Type $\times$ season	0.661	1	0.416
<b>Medium-sized dispersers</b>			
Type	6.876	1	0.008
Fragment (within type)	3.335	2	0.188
Season	10.324	1	0.001
Type $\times$ season	10.001	1	0.001
<b>Seed predators</b>			
Type	32.215	1	< 0.001
Fragment (within type)	7.580	2	0.023
Season	0.232	1	0.630
Type $\times$ season	10.315	1	0.001
<b>Seed dispersal rate</b>			
Type	0.452	1	0.501
Fragment (within type)	0.491	2	0.782
Month	31.47	4	< 0.001
Season	28.499	1	< 0.001
Type $\times$ month	200.203	4	< 0.001
Type $\times$ season	99.286	1	< 0.001

we established 10 plots with four seed collectors (traps) as explained above. Overall, we installed 40 plots and 160 collectors. Plots were distributed homogeneously throughout the fragments; the mean distance ( $\pm$  SD) between traps within plots was  $10.9 \pm 2.5$  m. The four traps in each plot were placed in four distinct microhabitats considered as suitable places for birds to perch and drop seeds (e.g. Rey and Alcántara, 2000; González-Varo et al., 2008; Parejo-Farnés et al., 2017): (i) under female *P. lentiscus* plants, (ii) under male *P. lentiscus* plants, (iii) under the canopy of other shrub species with endozoochorous fruit (mainly *M. communis*, *Quercus coccifera* and *C. monogyna*), and (iv) on open ground under the tree canopy (*Pinus pinea*). We placed the collectors in October (at the beginning of fruit ripening) and recorded the seeds dispersed until March–April, after which point no more seeds were recorded.

## 2.7. Statistical analysis

We used generalized linear models (GLMs) to test the relative effects of type of forest fragment (connected vs. isolated) and season (mast vs. non-mast year) on the initial fruit abundance per individual plant and on the abundance of seed dispersers and predators. We included fragment identity as a nested factor within forest fragment type, as well as the interaction between the main factors, to test for seasonal consistency in the response variables. For initial fruit abundance we used a Gamma distribution, and for seed disperser and predator abundance, we used Poisson distributions, all of them with a log-link function for

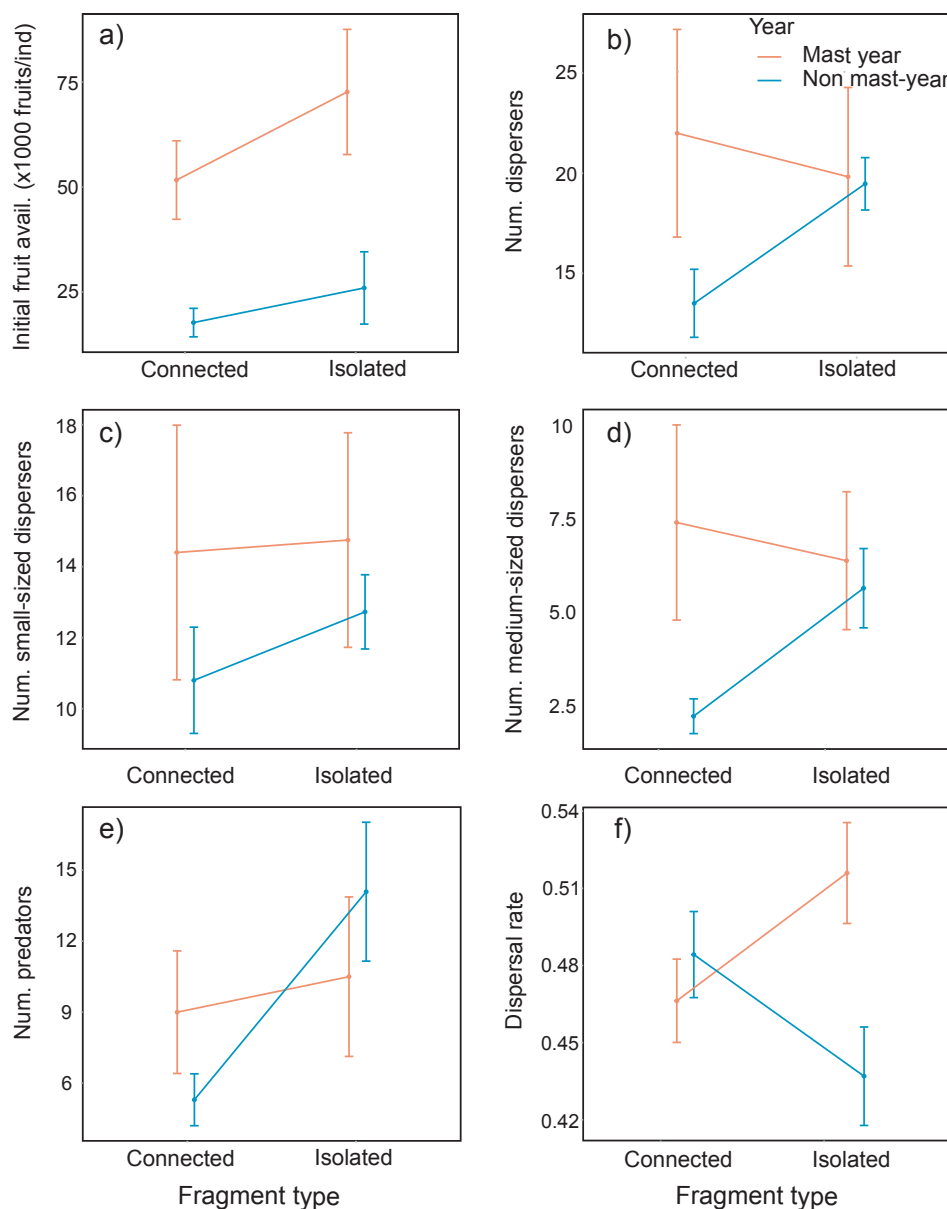
model fitting. For both the abundance of dispersers and predators the replicate unit of analysis was the individual transects carried out in each forest fragment. The significance of all categorical fixed-effects was assessed with likelihood ratio tests (LRTs) by comparing the full model with competing models, dropping one term at a time. Furthermore, we conducted the same GLM design with the response variable “dispersers abundance”, divided into small- and medium-sized dispersers abundance fractions.

Seed removal and seed predation rates were analyzed by fitting generalized linear mixed models (GLMMs) with fragment type (connected vs. isolated) as the main factor and fragment identity nested within fragment type. Temporal variation was accounted for in the model to detect intra-seasonal patterns with the factor month, and inter-seasonal differences with the factor season. Since we were also interested in the consistency of patterns of seed removal and predation between fragment types over time at both short and long temporal scales, we also included the two-way interactions between fragment type  $\times$  month and fragment type  $\times$  season. The proportion of dispersed seeds in each survey was fitted to a binomial distribution with a logit-link function, while the number of valves in the collection trays was fitted to a Poisson distribution with a log-link function to assess predation rates. The replicate units of analysis were the results of each survey of each focal plant (branches or collectors for dispersal and predation rates, respectively); as we had several measurements for each plant during the experiment we included plant identity as a random factor in the models. The significance of the main term and interactions was assessed with LRTs by comparing the full model with competing models dropping one term at a time. GLM and GLMM models were run with the package *lme4* (Bates et al., 2015) in R 3.3.2 (R Core Team, 2017).

Because of the large number of zeros in the seed rain dataset (in 63.8% of our visits we recorded no seeds in the collectors) and to avoid overdispersion in the models, the number of seeds in the collectors was fitted with a zero-inflated Poisson (ZIP) (Lambert, 1992) mixed model under a Bayesian framework (Zuur et al., 2012). The ZIP model was fitted as a two-part modeling approach: a binary model (i.e. a Bernoulli process with a logit-link function) and a count process modeled with a Poisson distribution (through a log-link function). We only included the intercept in the Bernoulli process due to the fact that the inclusion of covariates in this part leads to excessive model complexity and may suffer from estimation problems (see Zuur et al. (2012)). In the count process we included fragment type, fragment identity (nested within fragment type), year, and month as fixed covariates. As in previous analyses, we also included the two-way interactions between fragment type and the temporal covariates in the analysis to test for differences in seed arrival patterns between fragment types over time. Microhabitat and its interaction with fragment type were also included to test for differences in the final destination of seeds under contrasting fragmentation scenarios. We used the number of recorded seeds in each collector per survey as the replicate unit for analysis. Plot identity was included in the analysis as a random factor to account for the local-scale spatial-dependency structure. Priors for regression parameters and random intercepts were drawn from a diffuse normal distribution (mean = 0; precision = 0.0001). We ran three MCMC chains, with a burn-in of 10,000 iterations followed by 50,000 iterations and a thinning rate of 10. Convergence of MCMC chains was checked with the Gelman–Rubin statistic and the visualization of the plots of the chains for each estimated parameter. For each parameter, we extracted the mean, standard error, and 95% credible interval from the resulting posterior distributions carried out in JAGS (Plummer, 2003) in R with the package *R2JAGS* (Su and Yajima, 2015).

## 3. Results

As expected, initial fruit availability differed between seasons (Tables 1 and S2, Fig. 2a). During the mast season *P. lentiscus* yielded a



**Fig. 2.** Model-fitted average means and 95% confidence intervals for (a) initial fruit availability, (b) disperser abundance, (c) small-sized disperser abundance, (d) medium-sized disperser abundance, (e) predator abundance, and (f) seed dispersal rates (proportion of fruits consumed by dispersers) during the two study seasons (mast year and non-mast year) by forest fragment type.

large crop and was basically the only species with fleshy fruit in the study fragments. The estimated mean ( $\pm$  SD) fruit production of *P. lentiscus* plants during the mast season was 62,150 fruit per individual (51,650 and 72,650 in connected and isolated fragments, respectively). By contrast, during the non-mast season fruit production dropped dramatically to an average of 21,803 fruit per individual (17,672 and 25,934 in connected and isolated fragments, respectively; Fig. 2a). Fruit production did not differ between fragment types (Tables 1 and S2, Fig. 2a).

### 3.1. Abundance of seed dispersers and predators

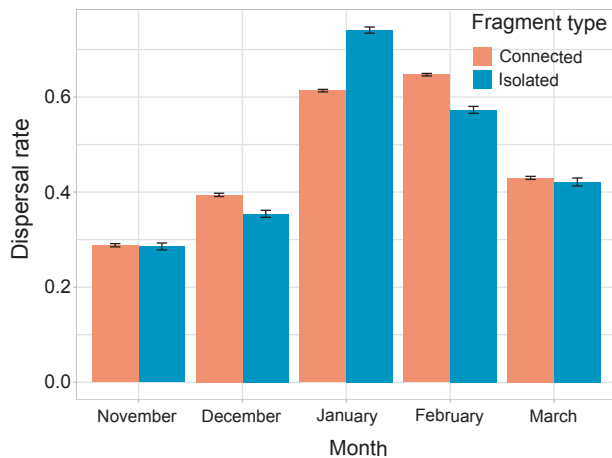
Overall, we recorded 958 birds (614 and 344 birds in the mast and non-mast years, respectively) belonging to 18 species (Table 2), eight disperser and 10 predator species, respectively. The most abundant disperser species recorded were *S. melanocephala*, *S. atricapilla*, *T. merula* and *E. rubecula*, which comprised 50%–63% of the total frugivorous bird abundance, and the most abundant predator species were

*Parus major*, *Carduelis chloris*, *Fringilla coelebs* and *Serinus serinus*, which comprised 21%–28% of the recorded birds. Overall, the abundance of seed dispersers was higher in the mast season, while fragment identity within fragment type was not significant, which shows that fragments of the same type displayed similar patterns (Tables 1 and S2). We found a significant interaction in seed disperser abundance between fragment types (connected vs. isolated) and seasons (mast vs. non-mast): the abundance of seed dispersers was higher in connected than in isolated forest fragments in the mast season; however, the opposite trend was observed in the non-mast season, with a greater abundance in isolated than in connected forest fragments (Tables 1 and S2, Fig. 2b). Small-bodied dispersers were more abundant in the mast season and seemed to be less sensitive to fragmentation effects since no differences were found between fragment types (Tables 1 and S2). Medium-sized dispersers generally showed the same behavior as the set of all dispersers: there was an interaction between fragment type and season (Tables 1 and S2) but they were more abundant in isolated forest fragments depending on the availability of fruits, as revealed by the significant

**Table 2**

Mean values ( $\pm$  SD) and total abundances of frugivorous bird species (dispersers and predators) in two seasons (mast and non-mast years) in the studied forest fragments. Of the legitimate dispersers, small-sized (S) and medium-sized (M) dispersers are indicated.

Bird species	Connected fragments				Isolated fragments			
	CHN		HNJ		CRB		VIS	
	Mast year	Non-mast year	Mast year	Non-mast year	Mast year	Non-mast year	Mast year	Non-mast year
<b>Seed dispersers</b>								
<i>Sylvia atricapilla</i> (S)	4.3 $\pm$ 0.6	1.6 $\pm$ 1.5	2.4 $\pm$ 0.5	0.9 $\pm$ 1.4	5.3 $\pm$ 2.1	3.0 $\pm$ 1.9	2.0 $\pm$ 1.9	0.9 $\pm$ 1.2
<i>Sylvia melanocephala</i> (S)	4.0 $\pm$ 1.0	2.9 $\pm$ 1.2	2.2 $\pm$ 1.9	2.7 $\pm$ 0.7	1.6 $\pm$ 1.0	3.2 $\pm$ 1.1	4.3 $\pm$ 2.1	2.7 $\pm$ 1.4
<i>Turdus merula</i> (M)	1.7 $\pm$ 0.6	1.0 $\pm$ 0.8	1.8 $\pm$ 1.3	1.0 $\pm$ 0.9	1.2 $\pm$ 0.7	0.6 $\pm$ 0.7	3.0 $\pm$ 2.4	2.1 $\pm$ 1.2
<i>Erithacus rubecula</i> (S)	2.7 $\pm$ 2.1	2.7 $\pm$ 1.8	3.2 $\pm$ 1.9	1.9 $\pm$ 1.4	0.9 $\pm$ 1.1	1.6 $\pm$ 1.3	2.6 $\pm$ 2.6	1.5 $\pm$ 1.0
<i>Phoenicurus ochruros</i> (S)	0.3 $\pm$ 0.6	0.3 $\pm$ 0.5	0.2 $\pm$ 0.4	0.8 $\pm$ 1.0	0.3 $\pm$ 0.5	–	0.3 $\pm$ 0.5	0.1 $\pm$ 0.3
<i>Turdus philomelos</i> (M)	0.7 $\pm$ 1.2	0.3 $\pm$ 0.8	3.6 $\pm$ 3.9	0.4 $\pm$ 0.9	1.7 $\pm$ 2.7	1.7 $\pm$ 2.2	–	1.2 $\pm$ 1.6
<i>Columba palumbus</i> (M)	–	0.1 $\pm$ 0.4	–	0.3 $\pm$ 0.5	1.9 $\pm$ 3.8	–	–	0.6 $\pm$ 1.0
<i>Sturnus vulgaris</i> (M)	–	1.1 $\pm$ 1.1	0.6 $\pm$ 1.3	–	–	0.3 $\pm$ 0.7	–	0.1 $\pm$ 0.3
<b>Seed predators</b>								
<i>Parus major</i>	2.0 $\pm$ 1.7	0.9 $\pm$ 0.9	3.8 $\pm$ 1.8	0.2 $\pm$ 0.4	2.0 $\pm$ 1.3	1.9 $\pm$ 1.4	3.0 $\pm$ 1.2	0.6 $\pm$ 0.8
<i>Carduelis chloris</i>	–	0.7 $\pm$ 1.0	0.2 $\pm$ 0.4	0.4 $\pm$ 0.9	0.3 $\pm$ 0.5	1.1 $\pm$ 1.2	1.3 $\pm$ 1.5	1.3 $\pm$ 1.9
<i>Fringilla coelebs</i>	3.3 $\pm$ 4.2	0.3 $\pm$ 0.5	0.8 $\pm$ 1.8	0.8 $\pm$ 1.1	1.0 $\pm$ 1.9	0.4 $\pm$ 0.7	0.9 $\pm$ 1.2	0.4 $\pm$ 1.0
<i>Serinus serinus</i>	0.7 $\pm$ 1.2	0.4 $\pm$ 0.8	0.0 $\pm$ 0.0	0.4 $\pm$ 0.7	–	1.7 $\pm$ 1.6	0.1 $\pm$ 0.4	0.5 $\pm$ 1.0
<i>Passer domesticus</i>	–	–	–	–	–	1.9 $\pm$ 5.3	2.9 $\pm$ 7.6	2.3 $\pm$ 5.1
<i>Carduelis cannabina</i>	0.3 $\pm$ 0.6	–	–	–	–	–	–	–
<i>Cyanistes caeruleus</i>	–	0.7 $\pm$ 0.8	–	0.1 $\pm$ 0.3	–	–	–	0.1 $\pm$ 0.3
<i>Cyanoptera cyanus</i>	–	1.7 $\pm$ 4.1	–	–	–	–	–	–
<i>Carduelis carduelis</i>	–	–	–	–	–	0.3 $\pm$ 0.7	–	0.8 $\pm$ 1.3
<i>Saxicola torquatus</i>	–	–	–	–	–	–	–	0.7 $\pm$ 1.6



**Fig. 3.** Model fitted means ( $\pm$  95%CI) of seed dispersal rates (proportion of fruits consumed by dispersers) by month and forest fragment type.

season effect.

We also observed an interaction in seed predator abundance between fragment types and season, with higher abundances in isolated forest fragments during the non-mast season (Table 1, Fig. 2e). A weaker but still significant relationship was observed between fragments, mostly due to the high abundance of predators in the VIS compared to CRB population in the first season (Table S2).

### 3.2. Seed removal and predation rates

We detected a significant interaction between temporal factors (month and season) and fragment type (Tables 1 and S3), indicating that seed removal was slightly higher in isolated fragments during the mast season; however, when the availability of fruits fell in the non-mast year the dispersal rates decreased in isolated compared to connected fragments (Fig. 2f). In other words, seed removal was less variable between seasons in connected fragments but more variable in isolated fragments. Within seasons, there was a marked monthly

variability in dispersal patterns, with most dispersal events occurring in January–February and with non-overlapping peaks between fragment types (connected and isolated) (Fig. 3).

Overall, the predation rate in *P. lentiscus* averaged only 0.4% of the fruit crop in the four forest fragments in the two study seasons (results of the GLM on predation rates can be found in Tables 1 and S4).

### 3.3. Seed rain across microhabitats and years

As expected, due to the masting pattern of *P. lentiscus*, the number of seeds collected in the two study seasons was different (Tables 3 and S5): 1084 seeds were recorded in the collectors during the mast season but only 249 in the non-mast season (all fragments pooled). However, no significant differences were detected in the number of seeds collected either between fragment type or fragment. Overall, there were differences between the *Pistacia* female microhabitat and the other microhabitats (Tables 3 and S5, since more than one half of the dispersed seeds were located under the maternal plant (60% in the mast season and 55% in the non-mast season). We found no differences between months (Table 3, Fig. 4) since a similar number of seeds were recovered in the collectors in each visit during the dispersal season. Unexpectedly, patterns of seed deposition across microhabitats and months did not differ according to fragment type (Table 3) and all showed the same trend, with overlapping 95% credible intervals for the estimated parameters (Fig. 4).

## 4. Discussion

In this study we found a greater abundance of seed dispersers in connected than in isolated forest fragments during the mast season but the opposite pattern in the non-mast season. However, small seed dispersers, which are responsible for most dispersal events, showed no differences in abundance. We detected a higher abundance of seed predators in isolated fragments and thus we would have expected to find lower rates of seed removal by legitimate seed dispersers in isolated fragmented forests than in connected forest fragments. However, we did not find that seed removal rates were affected by fragmentation due to the decoupling of plant–frugivore interactions. These decoupled

**Table 3**

Posterior mean values, standard errors (SE), and 95% credible intervals (95% CI) of the main factors of the Bayesian zero-inflated Poisson (ZIP) mixed model of the seed rain of *P. lentiscus*. Values for regression parameters of the interaction terms are omitted (see Fig. 4). Important terms (those whose 95% credible intervals do not overlap zero) are highlighted in bold.

Parameters	Covariate	Mean	SE	95% CI
<i>Count process (Poisson distribution with log-link function)</i>				
$\beta_0$	Intercept	1.470	0.174	(1.112, 1.805)
$\beta_1$	Type (isolated vs. connected fragments)	-0.329	0.246	(-0.808, 0.159)
$\beta_2$	Season (non-mast vs. mast year)	-1.116	0.117	(-1.342, -0.885)
$\beta_3$	Microhabitat (male vs. female)	-1.345	0.142	(-1.625, -1.069)
$\beta_4$	Microhabitat (shrub vs. female)	-1.258	0.156	(-1.564, -0.957)
$\beta_5$	Microhabitat (tree vs. female)	-2.148	0.189	(-2.528, -1.785)
$\beta_6$	Month (December vs. November)	0.194	0.125	(-0.051, 0.441)
$\beta_7$	Month (January vs. November)	0.099	0.128	(-0.149, 0.349)
$\beta_8$	Month (February vs. November)	0.239	0.125	(-0.007, 0.482)
$\beta_9$	Fragment HNJ vs. CHN (nested within fragment type connected)	-0.255	0.216	(-0.670, 0.166)
$\beta_{10}$	Fragment VIS vs. CRB (nested within fragment type isolated)	0.084	0.214	(-0.334, 0.505)
$\sigma_{\text{plot}}$	Random term for plot effect	0.427	0.068	(0.309, 0.575)
<i>Binary process (Bernoulli distribution with logit-link function)</i>				
$\gamma_0$	Intercept	-0.675	0.130	(-0.945, -0.435)

responses are mostly due to the high feeding dependence of disperser birds on *P. lentiscus* fruit.

#### 4.1. Abundance of seed dispersers and predators

The most abundant frugivorous bird species were the legitimate dispersers *S. melanocephala*, *S. atricapilla*, *T. merula* and *E. rubecula*. This agrees with both the classic studies conducted on seed removal process in *P. lentiscus* (Jordano, 1989; Verdú and García-Fayos, 1996) and with recent studies using DNA barcoding techniques that have assessed the identity of the dispersal agents of *P. lentiscus* (González-Varo et al., 2014, 2018; Parejo-Farnés et al., 2018). We found differences in the presence of dispersers between years associated with differences in fruit production in *P. lentiscus*, a pattern found in other masting species. For example, changes in disperser abundance in *Olea europaea* varied with the fruit supply (Jordano, 1987). As expected, the abundance of seed dispersers was higher in the masting season, which had a greater seed removal rate, suggesting a strong association between fruit production and the abundance of dispersers. Legitimate bird dispersers are specialists on *P. lentiscus* as they feed almost exclusively on these lipid-rich fruit (Jordano, 1985). On the other hand, the abundance of predators was similar between fragment types, regardless of the masting pattern. This can be explained by the typical generalist feeding habits of seed predators, which are less dependent on the availability of *P. lentiscus* fruits (Blondel and Aronson, 1999). During the non-mast season there was a greater abundance of dispersers and predators in isolated than in connected fragments, which we attribute to the fact that both are residents throughout the year.

Habitat fragmentation usually changes the composition of the disperser guild and this effect is more visible for medium-sized than small bird dispersers (Uriarte et al., 2011; Farwig et al., 2017). In our study area, medium-sized birds are represented by a few resident species throughout the year (mainly *Turdus* spp.). The size of the dispersers is important because medium-size birds are responsible for long-distance dispersal events since maximum dispersal distances depend not only on the distance that dispersers can travel but also on the size of seeds relative to their body mass and the time of retention of the seeds within their bodies (Jordano, 2017). In our area, we found that small bird dispersers (mostly *Sylvia* spp.) were less sensitive to fragmentation than medium-sized dispersers as they need fewer resources and are mostly temporary residents. They are responsible for most short-distance dispersal (SDD) events (Jordano et al., 2007). This result agrees with a previous genetic study carried out in the same forest fragments (Parejo-Farnés et al., 2017) where the authors found a very low effective number of mother plants ( $N_{em}$ ), which, in view of our results, must be attributable to SDD by small-sized birds. In an empirical study in

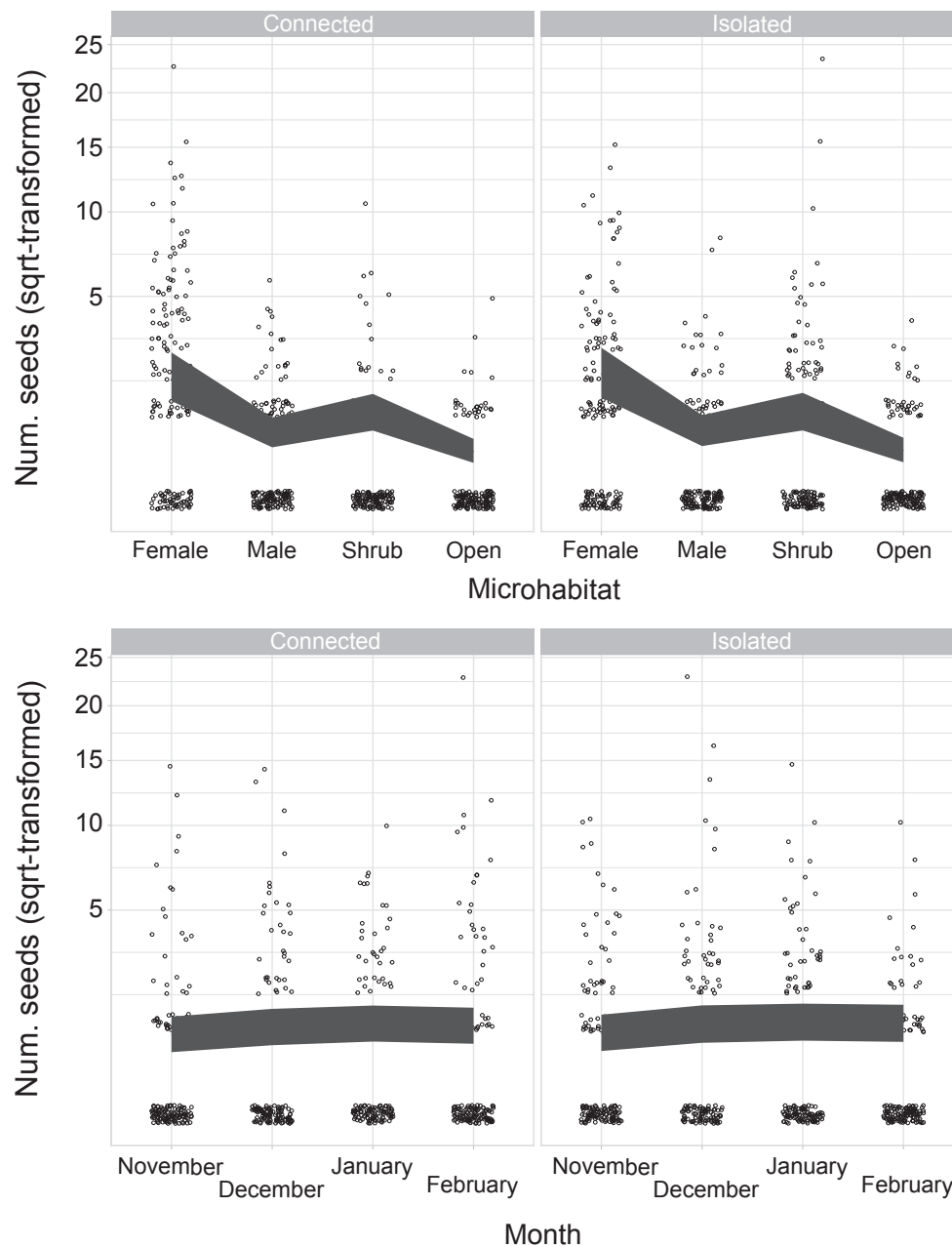
southern Spain, Jordano et al. (2007) found that small birds dispersed seeds less than 51 m from their origin, while birds of medium size dispersed up to 495 m. We believe that at our study site, having more medium-sized bird dispersers in isolated than in connected fragments will not ensure that the final destination of seeds is adequate due to the small size of the fragments and the inhospitable matrix that surrounds them (intensive crop fields) that impede the flow of birds between fragments. This is another characteristic of the study fragments that help us classify between connected and isolated, despite the fact that each one has a different size and some characteristics of the connected ones have a permeable matrix (crops or forests) and the isolated ones are surrounded by plowed fields uncultivated.

#### 4.2. Seed removal and predation rates

Overall, the dispersal rates found in this study were relatively high (51% and 57% in mast and non-mast seasons, respectively). Previous studies in other non-fragmented populations have reported dispersal rates of 42%–91% (Jordano, 1989; Verdú and García-Fayos, 1995, 2002). There was a higher removal rate in isolated fragments in the mast season and the opposite pattern in the non-mast season. These results indicate that seed removal is relatively steady regardless of the degree of connectivity of these studied fragmented forests, and that seed removal patterns are mainly related to the difference in fruit availability between seasons. In a previous study, Herrera (1985) found that a few small-size dispersers (*E. rubecula*, *S. atricapilla* and *S. melanocephala*) accounted for most of the frugivory at each site and dispersed the majority of seeds. The differences in seed removal observed between the two types of fragments on a monthly scale are the result of changes in the food resources on offer.

The difference in the number of dispersers between connected and isolated fragments did not seem to affect seed removal rates. This result may be indicative of the absence of a satiation process in which the fruit crop is not completely depleted and is therefore not dispersed (e.g. Jordano, 1987). Results similar to ours were reported by Herrera and García (2010) in a fragmented landscape, where these authors found no differences in seed removal rates between fragment types (connected and isolated) but differences between years, which they attribute to the high mobility of birds. In a similar sense, Farwig et al. (2017) also found that the loss of vulnerable species did not result in reduced seed removal rates in fragmented as opposed to continuous temperate forests. However, after a process of anthropogenic landscape fragmentation this result is not universal and, for example, Alcántara et al. (1997) recorded lower dispersal rates in fragmented forests.

Predation rates were negligible in *P. lentiscus* compared to those reported in other studies of the same plant and with similar



**Fig. 4.** Posterior mean values (black lines) and 95% credible intervals (shaded areas) per microhabitat (upper panels) and month (lower panels) for each forest fragment type (connected and isolated) from the Bayesian ZIP mixed model superimposed on the observed values (points). Slight jittering was added to the points to avoid overplotting; the Y-axis was square root-transformed to improve visualization.

methodology (see Jordano, 1989; Verdú and García-Fayos, 1995, 2001). We found isolated individuals with predation rates of up to 7% but in general the average was extremely low (0.4% in the four fragments). Fruit predators are relatively much rarer than small-sized dispersers and they either eat fruit infrequently or fruit represent a negligible fraction of their diets (Herrera, 1985).

#### 4.3. Seed rain across microhabitats and years

The effects of habitat fragmentation on frugivorous birds and seed removal rates did not alter the amount of seeds recovered in fragment types. As expected, the distribution of dispersed seeds was strongly skewed, with most seeds deposited under the maternal plant. Dispersal under the maternal plant decreases the potential viability of seedlings due to competition with the mother plant and increases the levels of

post-dispersal seed predation (*i.e.* the Janzen–Connell effect). This result agrees with a previous work (Parejo-Farnés et al., 2017) in which low  $N_{em}$  were associated with high seed dispersal under the mother plant. Moreover, the effective short-distance frugivore-mediated seed dispersal observed here may be related to the greater abundance of small bird dispersers in both fragment types, thereby encouraging SDD, which reduces gene flow between populations. Although we recorded more medium-sized birds in isolated forests, this result was not reflected in the seed rain. The small size of the isolated fragmented forests and the strong territorial behavior of birds such as *E. rubecula* may limit dispersal movements within fragments so that they have no effect on the seed rain deposition pattern. In spite of the intensively managed condition of some of our studied fragments, seed rain was similar between fragments and independent of fragment type. This was an unexpected result but can be explained by the fact that, unexpectedly,



small-sized birds were equally abundant in all fragments.

Overall, in the three components of the seed removal processes in our study we found: (i) a high variability in fruit availability between years due to masting, (ii) the distance component was unaffected by isolation imposed by fragmentation, and (iii) disperser birds were affected by the degree of connectivity of the fragments, their abundances being lower in isolated forest fragments during the maximum fruiting season (mast season). This study emphasizes the importance of seasonality for understanding how environmental variables influence patterns of frugivore-mediated seed removal.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ppees.2020.125541>.

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