

## ARTICLE

## Seed dispersal effectiveness in fragmented and defaunated landscapes

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**Abstract**

Landscape fragmentation and defaunation have major impacts on plant dispersal and dynamics. However, whether the impact of such perturbations on seed dispersal and recruitment change in sign and strength across habitats and spatial scales, and whether they amplify or buffer each other, remains largely unknown. To evaluate, for the first time, the joint impact of fragmentation and defaunation on seed dispersal effectiveness (SDE) across spatial scales (e.g., short- and long-distance seed dispersal), we utilized the long-term field data of a mammal-dispersed tree (*Pyrus bourgaeana*) in a spatially explicit individual-based model. By means of simulation experiments, we evaluated the effects of different levels of landscape fragmentation and defaunation on SDE and tree recruitment. Our simulation results revealed that the direction and magnitude of the fragmentation effect on SDE depended on its strength (mild, severe) and the spatial scale considered. Severe fragmentation decreased SDE for short- and intermediate-distance seed dispersal. Interestingly, mild and severe fragmentation increased SDE of long-distance seed dispersal, suggesting a positive effect of such perturbations (i.e., an increase in the proportion of successful long-distance dispersal events). Though defaunation had a consistently negative effect on overall SDE, its magnitude was highly species- and spatial-scale-dependent. The impact of defaunation on seed dispersal distance was also species-specific: the proportion of long-distance dispersal increased under total badger (*Meles meles*) defaunation but decreased under total fox (*Vulpes vulpes*) defaunation. A pervasive integration of seed dispersal distance into the SDE framework is essential to most comprehensively understand the scale-dependent nature of human activity impacts on plant dynamics. In the long term, strong perturbations (landscape fragmentation and defaunation) could select either for or against long-distance seed dispersal, altering in different ways the ability of plants to cope with climate change.

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**KEYWORDS**

costs of dispersal, global change, habitat heterogeneity, long-distance seed dispersal, perturbations, recruitment, scale-dependent responses, seed mortality, simulation model

**INTRODUCTION**

Seed dispersal is a critical demographic process that strongly influences plant dynamics, the assembly of communities, and the functioning of many ecosystems. Seed dispersal is characterized by a myriad of costs and benefits (Bonte et al., 2012; Corlett, 2021; Fedriani & Delibes, 2011). Among the benefits, long-distance seed dispersal (while typically rare) assists plant dynamics by facilitating gene flow, the connection of subpopulations, range extension, and the (re)colonization of vacant habitats (Bacles et al., 2006; González-Varo et al., 2021; Nathan et al., 2008). Seed dispersal at short and intermediate distances is most frequent and tends to increase local recruitment and thus the long-term population persistence (Fedriani et al., 2012). Among the costs of seed dispersal, the arrival in unsuitable habitats and microhabitats is a pervasive and dominant one (Bonte et al., 2012; Levin et al., 2003). Other costs occur with dispersal mechanisms, such as the energy invested to develop specific dispersal attributes (hooks, pulp, etc.; Sorenson, 1986) and seed mortality during ingestion and digestion of plants dispersed inside frugivorous animals (i.e., endozoochory; e.g., Traveset, 1998).

Costs and benefits of seed dispersal are nicely integrated into the seed dispersal effectiveness (SDE; Schupp, 1993; Schupp et al., 2010) framework. SDE is ideally defined as the number of new adult plants produced by the dispersal activities of dispersers. SDE can be quantified as the number of seeds dispersed by dispersers (quantitative component) multiplied by the probability that a dispersed seed produces a new adult (qualitative component). Both quantitative and qualitative components account for costs and benefits of seed dispersal, for example, changes in the number of dispersed seeds and changes in the quality of seed deposition, respectively. In the long term, decreased SDE (i.e., increased costs and benefits ratio of seed dispersal) is expected to select against dispersal (Galetti et al., 2013; Gómez et al., 2021) and thus eventually to decrease dispersal rates, potentially augmenting resource competition, kin competition, and inbreeding in local populations (Bonte et al., 2012). Further, lower SDE in plant populations is expected to reduce plant adaptation to environmental change (Clark et al., 1999; Sales et al., 2021).

Intriguingly, environmental change can potentially modify both the quantity and the quality of seed dispersal (McConkey et al., 2012; Travis et al., 2013). In particular, both the expansion of unsuitable habitats (e.g., cultivations

and urban areas; Haddad et al., 2015; Jones et al., 2017) and increasing landscape fragmentation per se (i.e., an increase in the number of patches for a given amount of habitat; sensu Fahrig, 2017) could alter seed dispersal into suitable and unsuitable habitats. Though there is a comprehensive understanding of the impact of habitat loss on seed dispersal (Fontúrbel et al., 2015; Nield et al., 2020; Rodríguez-Cabal et al., 2007), only a handful of studies have evaluated the effects of habitat fragmentation per se (hereafter “fragmentation”) on seed dispersal and have provided mixed results (Cazetta & Fahrig, 2022). In the case of animal-dispersed plants, the quantity of dispersal events ending into unsuitable habitats depends on the movement patterns of seed dispersers and their habitat preferences (Morales & Morán López, 2022). For example, habitat-generalist and highly mobile dispersers, such as some carnivores, pigs, and other ungulates (Fedriani & Wiegand, 2014; Fragoso, 1997), tend to use many contrasting habitats in heterogeneous landscapes, thus leading to seed dispersal into unsuitable habitats (Anderson et al., 2011; Ehrlén & Morris, 2015). Further, suitable habitats will be usually located closer to source fruiting plants (than expected by a random distribution of fruiting plants) given that availability of different habitat types (with contrasting suitability) is usually to some degree spatially autocorrelated (McGarigal & Cushman, 2002). Consequently, the costs of seed dispersal in terms of seed arrival into unsuitable habitats and thus, SDE, will change in a nonlinear fashion with dispersal distance. Whether and how such a possible trend is altered by fragmentation remains unexplored partly because investigations of seed movement at landscape scales are very rare (Cazetta & Fahrig, 2022; Pegman et al., 2017).

Fragmented landscapes are often defaunated, that is, characterized by sparse populations of medium- and large-sized vertebrate seed dispersers (Dirzo et al., 2014). As a result of such scarcity of seed dispersers, plant populations in those human-altered landscapes tend to experience costs in terms of lowered quantity of seed dispersal, reductions of their seed dispersal kernels (Carlo et al., 2013; Fedriani et al., 2020), and ultimately declines in recruitment and establishment (Caughlin et al., 2015; Pires et al., 2018). In addition, very little is known concerning whether the effects of fragmentation and defaunation on seed dispersal change across habitats and spatial scales and whether they amplify or buffer each other (McConkey et al., 2012). Even less is known about the combined effect of both perturbations on plant

recruitment and establishment, which is important given that fragmentation often leads to defaunation (Liu et al., 2019). Addressing this concern requires experimentation at large spatial and temporal scales, as well as the removal of seed dispersers, which is logistically and ethically problematic. Fortunately, these limitations can be overcome by integrating long-term empirical data with individual-based simulation models (Chetcuti et al., 2021; Langhammer et al., 2019; Pegman et al., 2017).

Here, we investigate, for the first time, whether and how landscape fragmentation and defaunation alter overall SDE, as well as its quantitative and qualitative components at different spatial scales (e.g., long- and short-distance dispersal). We frame our study in an endozoochorous system, which is comprised of the Iberian pear, *Pyrus bourgaeana*, and its main seed dispersers, the red fox, *Vulpes vulpes*, and the Eurasian badger, *Meles meles*, in a highly heterogeneous Mediterranean landscape of southwestern Spain (Fedriani et al., 2020). To this end, we coupled long-term field data with a spatially explicit, individual-based simulation model (*DisPear*; Fedriani et al., 2018, 2020).

We performed model simulations to investigate the quantity and quality components of SDE that our focal plant population receives from its dispersal agents under different scenarios. We predicted that increased fragmentation would alter habitat use by seed dispersers and thus also the habitats where seeds are most often deposited. Defaunation was expected to reduce the number of dispersed seeds and, due to disperser species-specific habitat use, also the frequency at which seeds were dispersed to different habitat types. Thus, we investigate whether fragmentation and defaunation alter seed arrival in habitat types of contrasting suitability, the seed dispersal kernels (sensu Bullock et al., 2017), and tree recruitment. Specifically, we addressed the following four questions: (1) Do costs and benefits of seed dispersal change with landscape fragmentation and defaunation and, if so, are such changes scale-dependent? (2) Do fragmentation and defaunation alter the tree seed dispersal distribution and, in particular, the proportion of long-distance seed dispersal events? (3) Does the combined effect of both perturbations alter tree recruitment (i.e., overall SDE)? (4) Are the effects of fragmentation and defaunation on SDE additive or interactive?

## METHODS

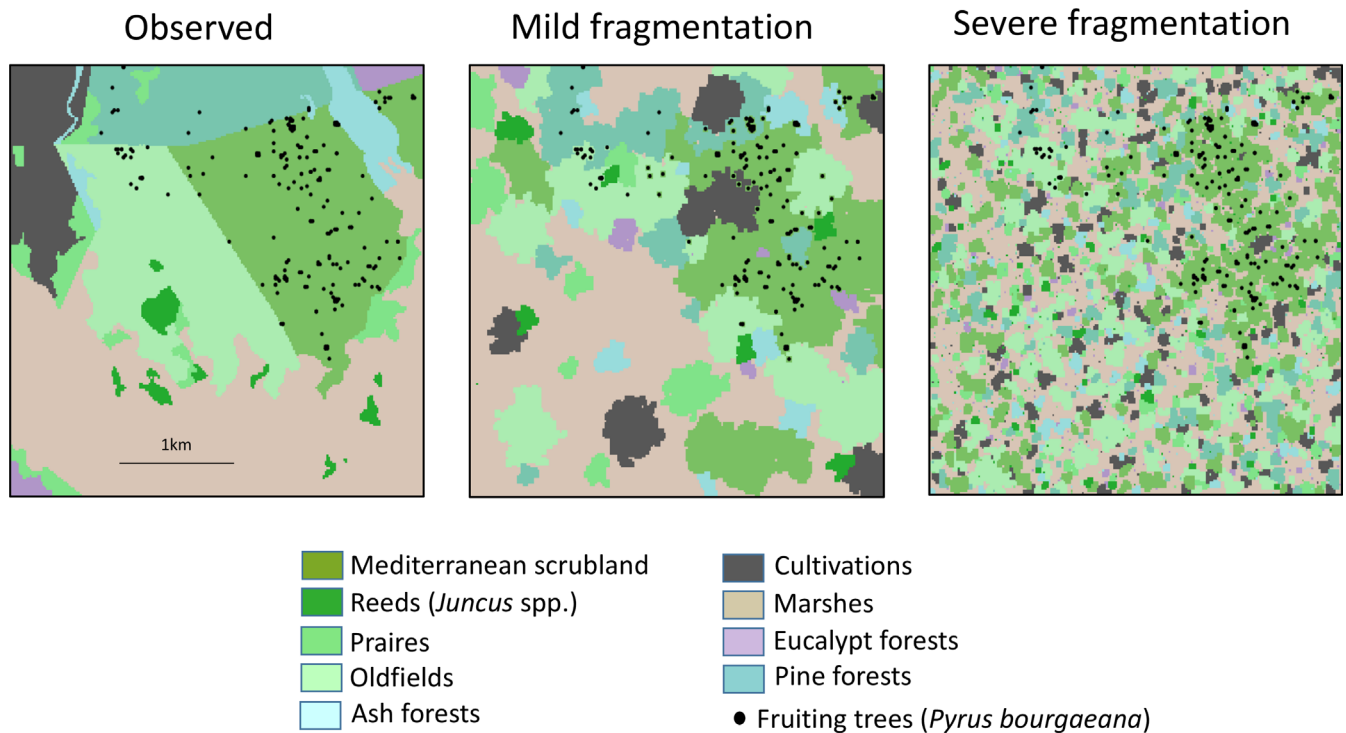
### Study system

Our study site (called Matasgordas and Coto del Rey) is located in the northern section of Doñana World

Biosphere Reserve, SW Spain (elevation 0–80-m above sea level [asl]). The climate is Mediterranean subhumid, characterized by dry, hot, long summers (June–September) and mild, wet winters (November–February). The average annual rainfall is 586 mm, with 84% occurring in autumn and winter, while the average monthly temperatures range from 10.0°C (January) to 24.7°C (July). Doñana habitats are highly heterogeneous (Figure 1). We grouped habitats based on their suitability for *P. bourgaeana*: (1) “Closed habitats” include the Mediterranean scrubland as well as scattered individuals and some small clumps of *Quercus suber*, *Fraxinus angustifolia*, *Olea europaea* var. *sylvestris*, and *Pinus pinea*. Closed habitats show the highest *P. bourgaeana* tree density, and the understory is dominated by *Pistacia lentiscus* shrubs. (2) “Open habitats” include oldfields as well as cultivations, some reeds (*Juncus* spp.) and prairies. This habitat type is being slowly recolonized by *P. bourgaeana*. (3) “Tree plantations” are represented by patches of *Pinus pinea* and *Eucalyptus* spp. forests. Adult *P. bourgaeana* trees are rare in this habitat. (4) “Marshes” are large seasonally flooded habitat, unsuitable for most terrestrial plants (including *P. bourgaeana*).

The Doñana area is undergoing continuous landscape fragmentation caused by varied human activities (e.g., García-Novo et al., 2007). In particular, *P. bourgaeana* distribution is very fragmented, with trees occurring at low densities (generally <1 individual ha<sup>-1</sup>) in some Mediterranean scrubland patches that are isolated from each other (from one to several kilometers) due to the presence of marshes, eucalypt plantations, or cultivations (Fedriani et al., 2010). Mortality of the most effective seed dispersers (badgers and foxes) is frequent due to illegal poaching, road kills, and other human-related causes (Fedriani et al., 2020; Revilla et al., 2001). Whether and how SDE of *P. bourgaeana* is impacted by fragmentation and whether such impact varies with defaunation levels has not been evaluated yet.

Both species of seed dispersers, specially badgers, feed on a variety of fruits during the autumn and early winter, including *P. bourgaeana* fruits (Perea et al., 2013). Habitat use and movements of foxes ( $n = 31$  individuals) and badgers ( $n = 17$  individuals) have been intensively investigated through telemetry (e.g., Fedriani et al., 1999) which provides a large dataset used for the parametrization of our model (see below). In general, during daytime, foxes and badgers are inactive and hidden in dens in closed habitats, while during sunset, they tend to move toward open habitats and marshes where they remain active during most of the nighttime (they rarely use tree plantations). Nonetheless, these seed dispersers differ in the relative use of the different habitat types and thus in the proportion of seeds dispersed into each habitat



**FIGURE 1** Observed landscape in the Doñana World Biosphere Reserve in SW Spain (left panel). Middle and right panels represent two examples of the study area under scenarios of additional mild and severe fragmentation, respectively. The area occupied by each habitat type as well as the number and location of adult *Pyrus bourgaeana* trees (black disks) remains fixed in all three scenarios. Other colors represent different habitat types: (1) marshes: pale brown (marshes); (2) closed habitats: green (Mediterranean scrubland) and cyan (ash forest); (3) open habitats: lime tones (oldfields, reeds, and prairies) and dark gray (cultivations); (4) tree plantation: turquoise (pine forest) and violet (eucalypt forests).

type (e.g., badgers use closed habitats more frequently than do foxes). Foxes and badgers show a high mobility (daily travel distances were  $2.15 \pm 2.21$  km, respectively) and relative long seed retention times (mean seed retention times were  $25.2 \pm 13.2$  and  $16.9 \pm 9.8$  h, respectively; Fedriani et al., 2018); these patterns are fully integrated into our model.

## The DisPear model

*DisPear* is a mechanistic, spatially explicit, individual-based model implemented in NetLogo 5.2.0. A complete, detailed model description following the Overview, Design concepts, Details (ODD) protocol (Grimm et al., 2006, 2010, 2020) is provided in Appendix S1. It includes information about the rationale and data underlying all model assumptions. The model was developed, parameterized, and tested following the pattern-oriented framework (sensu Grimm et al., 2005). Specifically, we used 46 patterns describing the dispersers' movement, foraging and social behavior, and physiology that were based on extensive field and experimental data collected over two decades by Fedriani et al. (2018).

The model includes six entities: habitat patches, dispersers, spatial groups of dispersers (i.e., the spatial area where different social groups of dispersers center their activities), fruiting pear trees, fruits, and feces. Dispersers are individual foxes and badgers that move across a heterogeneous landscape comprising of  $20 \times 20$  m<sup>2</sup> patches belonging to a given habitat type (closed, open, tree plantations, or marshes), eat the available ripe fruits dropped by the fruiting pear trees, and deliver the feces that contain the tree seeds. Dispersers belonged to one of two spatial groups, called northern and southern.

The model runs at a 1-h time step within a 75-day period that corresponds to the “dispersal season” (mid-September to the end of November) when ripe *P. bourgaeana* fruits are available to dispersers (Fedriani et al., 2012). The model is run for 25 years, each year representing the 75-day dispersal season only ( $25 \times 75 \times 24 = 45,000$  time steps). The model's spatial extent (total area is ~1840 ha) is a rectangular landscape of  $221 \times 208$  patches (Figure 1).

The model implements six main processes that are repeated every time step during a fruiting season (except when stated otherwise; Figure 2A). (1) Fruiting trees drop two to four ripe fruits at the beginning of the day

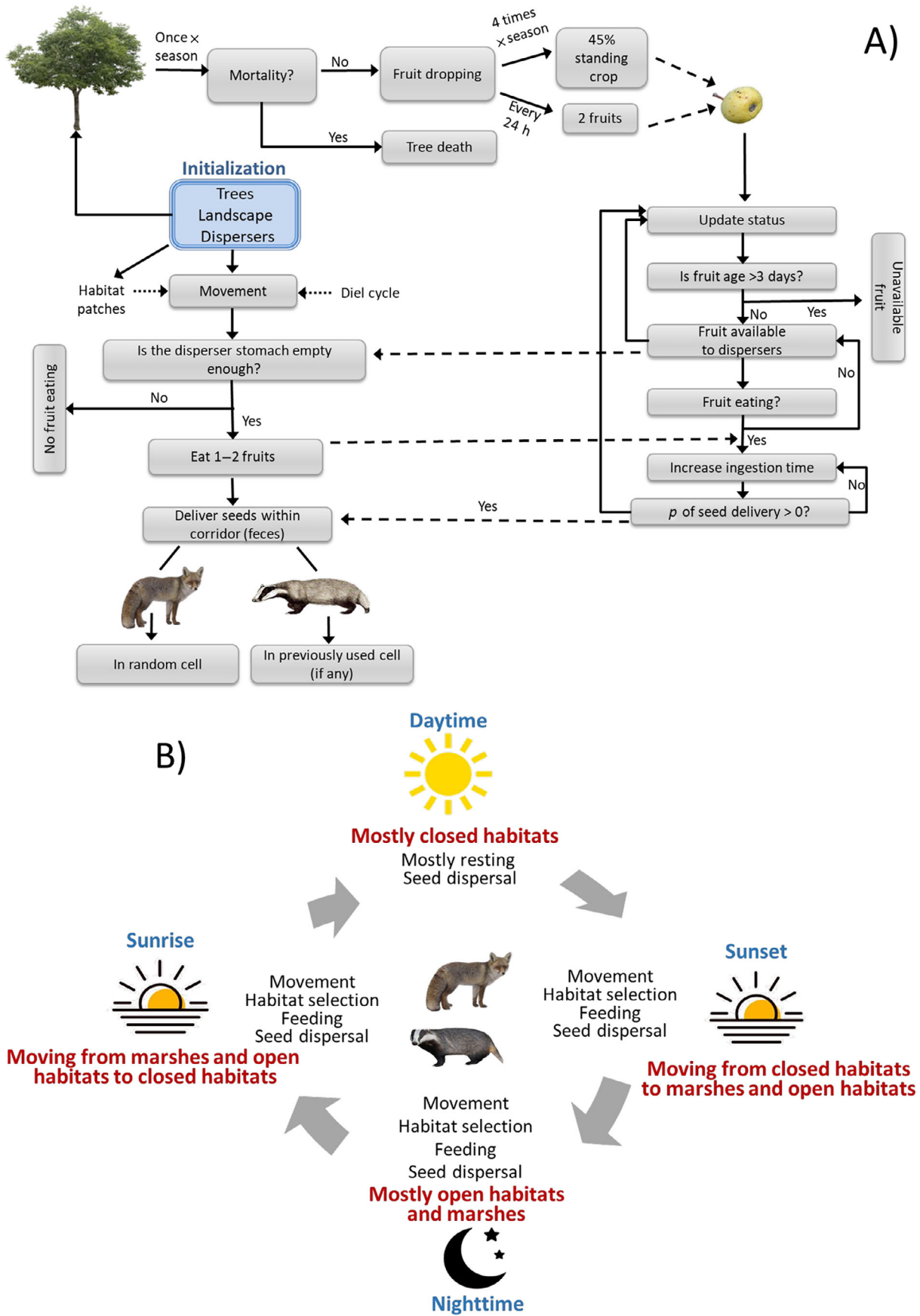


FIGURE 2 Legend on next page.

(i.e., once every 24 time steps) that become available to dispersers. (2) At every step (1-h), uneaten fruits on the floor increase their age becoming unavailable for dispersers after 3 days. Those that have been ingested (and not defecated yet) update their time in dispersers' digestive system. (3) Dispersers move to their species-specific preferred habitats according to circadian patterns (Figure 2B; Appendix S2). (4) Dispersers feed, based on empirical probabilities describing their foraging habits, if they are not satiated of fruit and there is a fruiting tree with available fallen fruits within a 200-m corridor along their movement path. (5) Dispersers might also defecate depending on the gut retention times of ingested fruits. Foxes defecate fruits (with seeds) by choosing randomly any cell within the corridor, and badgers defecate among those cells in which they had defecated before (if any) because they tend to repeatedly reused latrines. (6) At the end of a fruiting season, tree mortality takes place, surviving trees replenish their fruit crop, and existing fallen fruits and defecated feces are removed from the simulation. Since recruitment of adult trees is very infrequent in Doñana, we did not include recruitment of new reproductive trees (Figure 2A). Further details of the model processes are provided in Appendix S1 and Fedriani et al. (2018, 2020).

At the beginning of the simulation, the model is initialized in four steps: (1) The habitat type of patches and location of the fruiting trees are defined through an input file that represent the real landscape. (2) The crop size of each fruiting tree is randomly set through a Poisson distribution parameterized with field data. (3) The dispersers' spatial groups and their home ranges are defined. (4) Dispersers are created and located following rules described in the ODD.

## Landscape model and variables

To study the effects of fragmentation on seed dispersal, we created 1000 artificial landscapes (Figure 1). Landscape generation followed the methods of Railsback and Johnson (2014) via a stochastic process that kept the total number of patches of each habitat type (closed, open, tree plantations, or marshes) fixed but changed the number of clumps in which they were structured within the landscape. Only patches that do not have trees on them reset their habitat state variable, and a new habitat type was

assigned to them (Appendix S3). To quantify the level of fragmentation of real and artificial landscapes, we calculated the contagion index which characterizes whole landscapes (higher contagion represents lower fragmentation; McGarigal & Cushman, 2002). In addition to quantifying the availability of different habitat types surrounding fruiting *P. bourgaeana* trees (i.e., seed sources) at different distances, we calculated the O-ring statistic for each habitat type  $h$  and spatial scale  $r$  following Wiegand et al. (1999). We explored whether and how fragmentation altered the distribution of habitat types at different spatial scales and therefore the likelihood of seed dispersal into habitats of contrasting suitability. We used Pearson's  $r$  to test the correlation between O-ring and contagion index. For further details of landscape generation and variables, see Appendices S3 and S4.

## Seed dispersal effectiveness

We used the number of seed dispersal events for each habitat type (*DisPear* output) to calculate SDE. The quantitative component was defined as the overall number of dispersal events by each (or both) seed disperser species. The qualitative component was defined as the mean probability of recruitment averaged across all dispersal events (arriving at different habitat types). Then, overall SDE was defined as the number of dispersal events leading to recruits:

$$\sum_{i=1}^n N_i \times P_i,$$

where  $N_i$  is the total number of dispersal events for each habitat type  $i$ , and  $P_i$  is the probability of recruitment of a *P. bourgaeana* seed that arrives at habitat type  $i$ . The habitat-specific probabilities of recruitment after 14 months of seed deposition were calculated (during monthly checked field experiments using *P. bourgaeana* sowed seeds) by Fedriani et al. (2019) for tree plantations ( $p = 0.117$ ) and closed habitats ( $p = 0.037$ ) within the Doñana area. Also, we estimated the probability of recruitment in open habitats ( $p = 0.027$ ) by considering exclusively the subset of experimental blocks set by Fedriani et al. (2019) in open habitats. Fedriani et al. (2019) did not consider marshes as a potential habitat for *P. bourgaeana* recruitment. Based on our long-term

**FIGURE 2** Flowchart of the *DisPear* model (A) and details of the movement submodel showing typical activities and habitats used by seed dispersers (foxes and badgers) during daytime, sunset, nighttime, and sunrise (B). *DisPear* has six types of entities (dispersers [foxes and badgers], spatial groups, spatial units [i.e., cells], fruiting *P. bourgaeana* trees, fruits, and disperser feces containing dispersed seeds) and considers six main processes (fruit dropping, tree mortality, fruit change status, disperser movement, disperser fruit uptake, and disperser fruit delivery). See Appendix S1 for further details.

experience in this system, we assumed the probability of recruitment in this habitat is equal to zero ( $p = 0$ ).

Finally, we depicted the SDE landscapes (sensu Schupp et al., 2010) under target scenarios of fragmentation and defaunation (see below). SDE landscapes are two-dimensional representations of the possible combinations of the quantitative (number of seeds dispersed; x-axis) and the qualitative components of seed dispersal (number of recruits/number of seeds; y-axis). Isoclines connect all values of quantity and quality that yield the same SDE. Landscapes of SDE have typically been used to evaluate the contributions of different seed dispersers to the recruitment of different plant species (e.g., Gómez et al., 2021). Here, we extended the usage of SDE landscapes to estimate disperser's contribution to recruitment at different dispersal distances (e.g., short- and long-distance dispersal). Effectiveness landscape isoclines were plotted using the R package `effect.landscape` (Jordano, 2014) in Rstudio v.4.0.4. (R Core Team, 2021).

## Seed dispersal kernels

For each simulation, the distribution of seed dispersal distances (*DisPear* output) was pooled across individuals, disperser species, and years to estimate the dispersal kernel. A Weibull probability density function was fitted to the distributions by maximum likelihood estimation using the “`fitdistr`” function in the MASS package library (Ripley et al., 2022). We selected the Weibull distribution among other five candidate distributions (Appendix S5: Figure S1) based on standard quantitative approaches (e.g., Akaike information criterion). The Weibull distribution has two parameters, the scale (mean seed dispersal distance) and shape (i.e., kurtosis<sup>-1</sup>; low shape values equate to high kurtosis and “fat” long tails and vice versa). Further, seed dispersal events were classified based on dispersal distance as follows: (1) “short distance” ( $\leq 250$  m), corresponding to seed dispersal adjacent to tree clusters or among neighboring tree clusters; (2) “long distance,” for which we used an a priori absolute definition (sensu Nathan et al., 2008), being considered as those events with dispersal distance larger than 1 km—one or few kilometers is typically the separation among adjacent *P. bourgaeana* subpopulations in the area (the authors' unpublished data); and (3) “intermediate distance” ( $> 250$ – $1000$  m), corresponding to the remaining seed dispersal events.

## Simulation experiments

First, we ran a baseline scenario reproducing the observed landscape (Figure 1) and densities of seed

dispersers (five badgers and five foxes; Fedriani et al., 2020). Second, we studied the effects of increased landscape fragmentation (Figure 1) by using the 1000 random artificial landscapes (see section *Landscape model and variables* above) and running the simulations without defaunation (hereafter “fragmentation scenarios”). Third, we explored the impacts of defaunation by running simulations involving a reduction in the density of one carnivore species at a time by 40% (partial defaunation) and 100% (complete defaunation). Thus, we ran four scenarios that were replicated 100 times each. These simulations used the real landscape (hereafter “defaunation scenarios”). Fourth, we ran simulated scenarios where increased fragmentation and defaunation were combined (hereafter “combined scenarios”). We used a factorial design, running the four scenarios of defaunation (2 disperser species [fox and badger]  $\times$  2 defaunation levels [partial and total defaunation]) under two different scenarios of increased fragmentation (mild and severe fragmentation). To this end, each defaunation scenario was run selecting the 100 (out of 1000) artificial landscapes generated in the fragmentation-scenario analysis with the highest (“mild fragmentation”) and lowest (“severe fragmentation”) contagion indexes. Thus, our fragmentation treatments assume the occurrence of major perturbations (e.g., quarries and intensive agriculture; Camacho et al., 2022; Gürden, 2018) in the real landscape that would dramatically alter habitat suitability for most plant species and, in particular, for *P. bourgaeana*. In all scenarios, the locations of fruiting trees were held constant in our simulations; thus, the effect of our treatments could be safely linked to changes in habitat fragmentation and the number of seed dispersers but not to changes in tree location.

We analyzed the isolated and joint effects of fragmentation and defaunation on the quantitative and qualitative components of SDE, and on the overall SDE, as well as on dispersal distribution (i.e., kernels) after 25 years. To find out whether the effects of fragmentation and defaunation on seed dispersal were additive, we estimated response ratios following Darling and Côté (2008). For each isolated factor, and for their additive effects, the 95% confidence limits of their respective response ratios were calculated. Then, we compared the observed mean response ratio from the combined factors with the expected additive response ratio. If the observed response ratio from the combined factors fell below or above the 95% confidence limits of the additive response ratio, the effects were classified as non-additive, either increasing (synergistic) or decreasing (antagonistic) the expected cumulative negative impact on seed dispersal. Otherwise, the experiment was classified as additive. Because of the large number of replicates in our simulation experiments

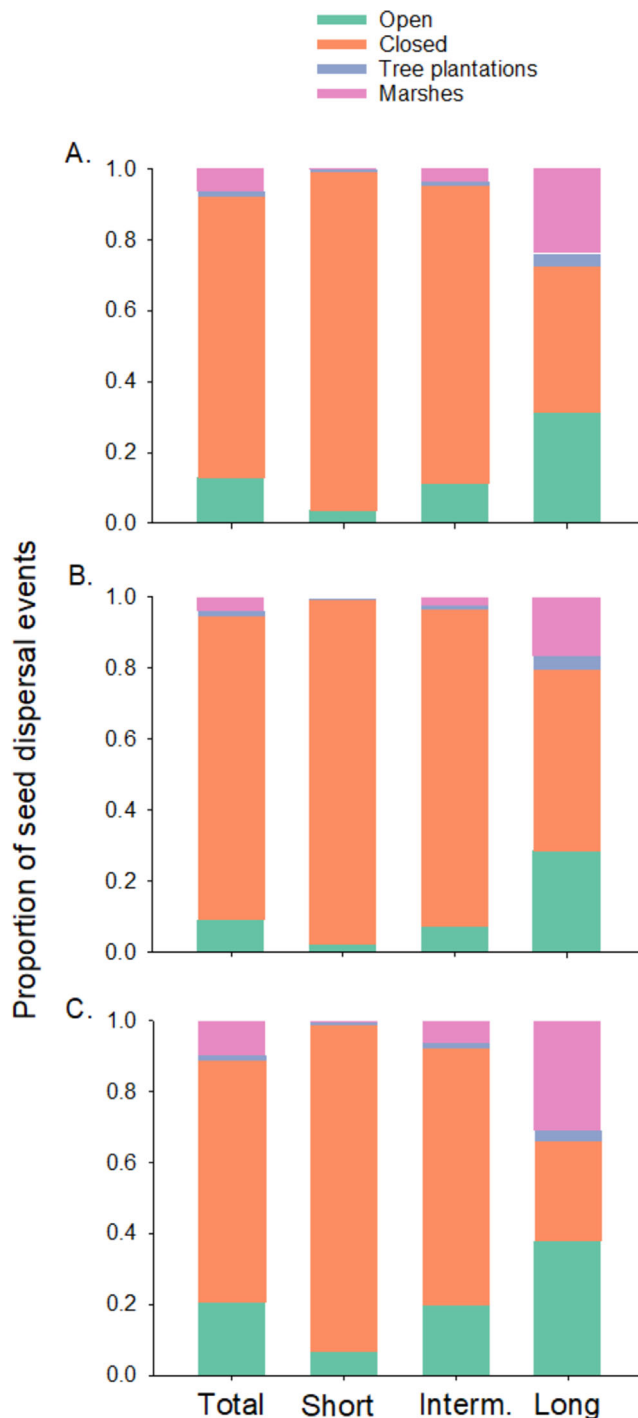
(100 for each scenario), even weak effects could be revealed as significant; thus, we did not perform typical statistical tests to contrast model outputs across the different scenarios (White et al., 2014).

## RESULTS

### Baseline scenario

Under the baseline scenario (no additional landscape fragmentation or defaunation), the mean quantity component over the 25-year simulated period was  $21,966 \pm 1262$  seed dispersal events (mean  $\pm 1$  SD). Most dispersed seeds arrived in closed habitats (79%), followed by open habitats (13%), marshes (6%), and tree plantations (2%; Figure 3A). Most short- and intermediate-distance dispersal events landed in closed habitats, whereas a large fraction of long distances dispersal events landed in marshes (24%) or open habitats (31%; Figure 3A). Given that marshes are unsuitable habitats, the quality of long-distance dispersal (i.e., proportion of seeds that recruit) was lower and much more variable ( $0.028 \pm 0.004$ ) than that for short- and intermediate-distance dispersal ( $0.037 \pm 0.0003$  and  $0.036 \pm 0.001$ , respectively; Figure 3A). Mean overall SDE for intermediate-distance dispersal ( $473 \pm 37$  dispersal events) was more than twice that for both short- ( $189 \pm 22$ ) and long-distance dispersal ( $102 \pm 21$ ; Figure 4A). The seed dispersal kernels showed a leptokurtic shape (Figure 4B), with most dispersal events (60%) taking place over intermediate distances, followed by short (23%) and then by long distances (17%; Appendix S6: Figure S1A).

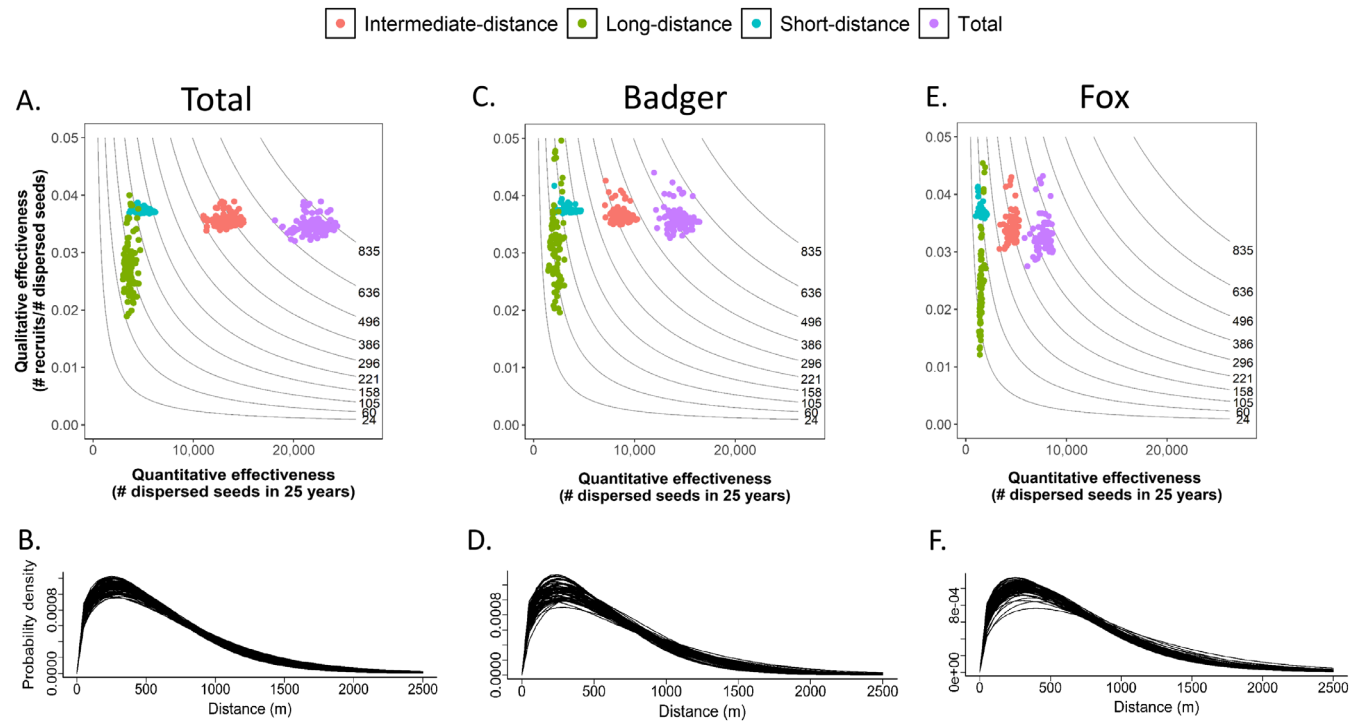
Overall, badgers dispersed more seeds than did foxes, but this pattern was inconsistent across habitat types. Specifically, badger dispersed 2.5 times more seeds than foxes into closed habitats but dispersed less into open habitats (0.77 times), marshes (0.75 times), and tree plantations (0.59 times; Figure 3B,C). Whereas the badger mean quantitative component ( $14,425 \pm 979$ , number of dispersal events) was 1.9 times larger than that of foxes ( $7802 \pm 573$ ), badger ( $0.036 \pm 0.002$ ) and fox ( $0.033 \pm 0.003$ ) mean qualitative components were similar (Figure 4C,E). The lowest quantitative component values were found for long- and short-distance dispersal for both badgers and foxes (Figure 4C,E). For both the seed dispersers, the qualitative component (i.e., proportion of seeds that recruit) was lower for long-distance dispersal ( $0.031 \pm 0.006$  and  $0.024 \pm 0.007$ ) compared with both short- ( $0.038 \pm 0.001$  and  $0.037 \pm 0.001$ ) and intermediate-distance dispersal ( $0.037 \pm 0.001$  and  $0.034 \pm 0.002$ ) for badger and fox, respectively (Figure 4C,E), partly due to a higher seed arrival in marshes (Figure 3B,C). The mean overall SDE for



**FIGURE 3** Proportion of seed dispersal events by habitat of seed arrival and dispersal distances (short distance,  $\leq 250$  m; intermediate distance,  $>250$ – $1000$  m; long distance,  $>1$  km) under the baseline scenario (neither additional fragmentation nor defaunation). (A) Considering seed dispersal by both red fox *Vulpes vulpes* and Eurasian badger *Meles meles*, (B) only seed dispersal by the Eurasian badger, and (C) only seed dispersal by the red fox.

badgers ( $520 \pm 41$ ) was two times greater than for foxes ( $256 \pm 27$ ; Figure 4C,E). Finally, although foxes showed a slightly higher proportion of long-distance seed dispersal





**FIGURE 4** Seed dispersal effectiveness (SDE) landscapes and dispersal kernels under baseline scenario (neither additional fragmentation nor defaunation) considering seed dispersal by both red fox *Vulpes vulpes* and Eurasian badger *Meles meles* (A, B), considering only seed dispersal by the Eurasian badger (C, D), and considering only seed dispersal by the red fox (E, F). The quantitative component of SDE corresponds to the number of dispersal events. The qualitative component of SDE corresponds to the number of recruits (benefits) divided by the total number of dispersal events (i.e., recruits plus seeds that fail to recruit). Note the change of scale in the isolines representing areas of equal overall SDE. In the kernel panels (B, D, F), each line represents the dispersal kernel of one out of 100 simulations.

than badgers (19% vs. 15%; Appendix S6: Figure S1A), the seed dispersal kernels of both species were rather similar (shape and scale parameters were  $1.4 \pm 0.1$  and  $650.2 \pm 57.8$  m [badger] and  $1.4 \pm 0.1$  and  $710.7 \pm 40.7$  m [fox]; Figure 4D,F).

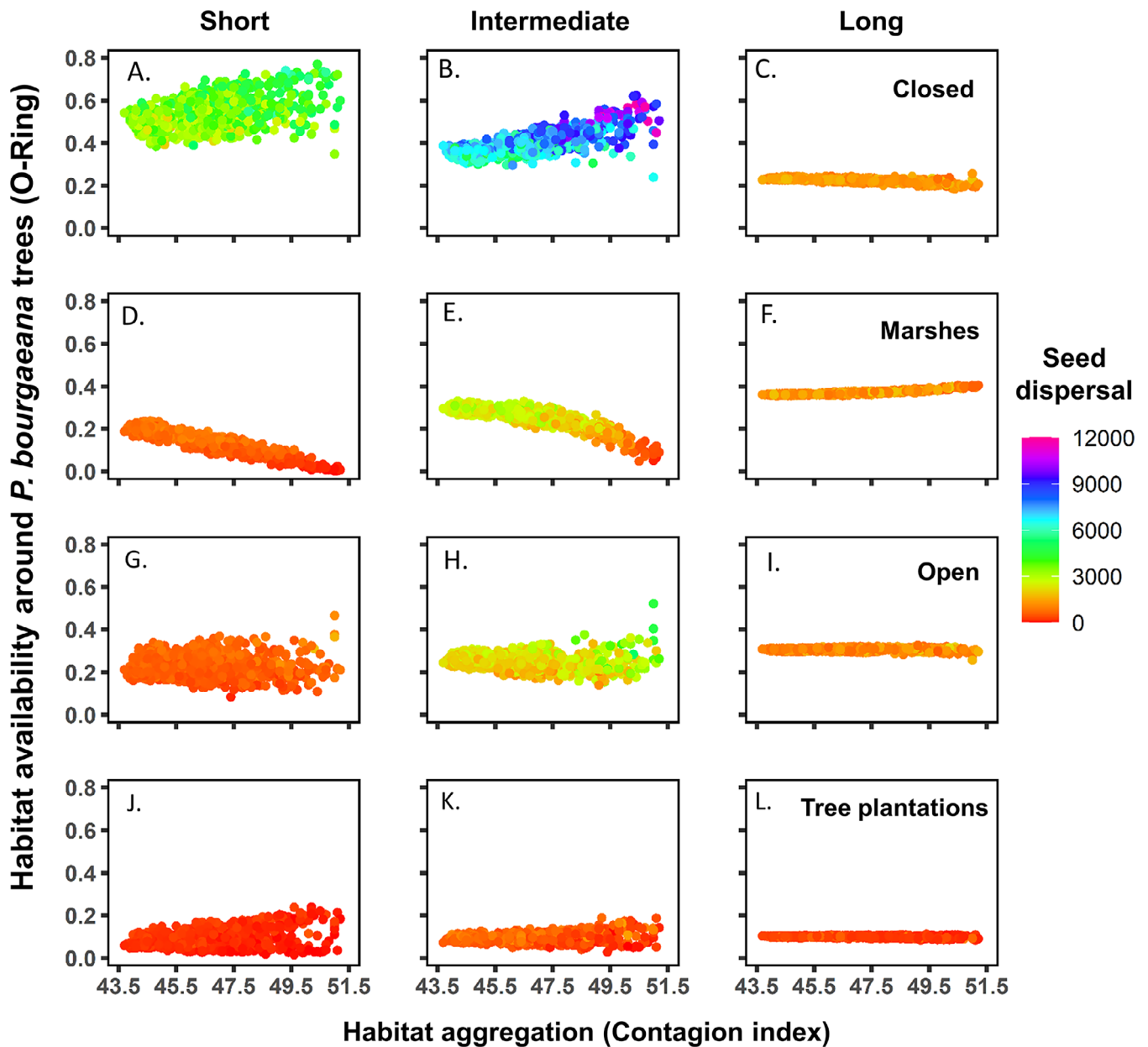
### Habitat availability around trees changed with fragmentation and spatial scale

We evaluated whether and how fragmentation altered the distribution of habitat types at different spatial scales and, in turn, the likelihood of seed dispersal into different habitat types. The relationship between the contagion index and the O-ring was highly dependent on the habitat type and spatial scale (Figure 5). Increasing fragmentation (i.e., decreasing contagion index), in relation to the baseline scenario, decreased significantly the proportion of closed habitat patches around fruiting trees (O-ring<sub>closed</sub>) at short (<250 m) and intermediate (250–1000 m) spatial scales but increased such proportion at the largest scale (>1000 m; Figure 5A–C). The exact opposite pattern was observed for marshes

(Figure 5D–F). Finally, changing fragmentation levels did not modify significantly the proportion of open habitats (O-ring<sub>open</sub>) and tree plantations (O-ring<sub>Treeplantations</sub>) around fruiting *P. bourgaeana* trees at any spatial scale (Figure 5G–L). Overall, all of these results indicate that fragmentation altered the representation of habitat types at different scales; this, in turn, affected seed dispersal across spatial scales and habitat types (Figure 5). For instance, whereas the number of intermediate-distance dispersal events arriving into closed and open habitats decreased with fragmentation (i.e., larger O-ring<sub>closed</sub> and O-ring<sub>open</sub>; Figure 5B,H), the number of intermediate-distance dispersal events arriving into marshes increased with fragmentation (i.e., lower O-ring<sub>marshes</sub>; Figure 5E).

### Isolated effects of landscape fragmentation and defaunation on SDE and dispersal kernels

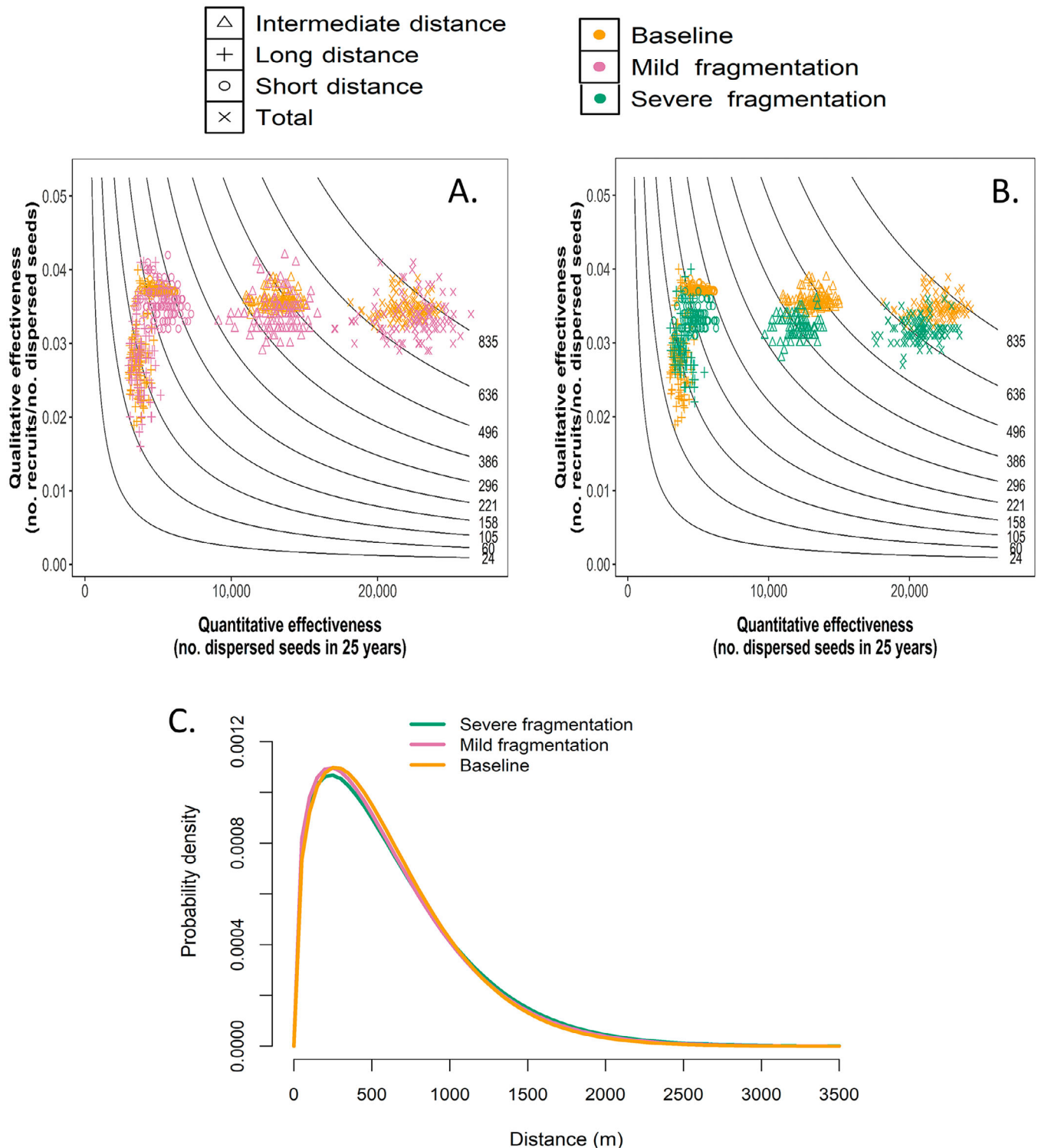
The effect of fragmentation on SDE depended on its strength (mild and severe) and the spatial scale



**FIGURE 5** Relationship between contagion index (higher contagion represents lower fragmentation), the O-ring (i.e., proportion of each habitat type around fruiting *Pyrus bourgaeana* trees), and the number of dispersal events for each habitat type (A–C, closed habitats; D–F, marshes; G–I, open habitats; J–L, tree plantations) and spatial scale (short distance,  $\leq 250$  m; intermediate distance,  $>250$ – $1000$  m; long distance,  $>1$  km).

considered (Figure 6A,B). Specifically, (1) under severe fragmentation, the mean overall SDE for total ( $661 \pm 53$  seed dispersal events; mean  $\pm$  1SD), short ( $160 \pm 23$ ), and intermediate-distance dispersal ( $387 \pm 33$ ) decreased by 13%, 15%, and 18% relative to the baseline values ( $763 \pm 56$ ,  $189 \pm 22$ , and  $472 \pm 37$ , respectively) due to decreases in both the quantity and the quality of seed dispersal, (2) under both mild and severe fragmentation, the mean overall SDE of long-distance dispersal ( $111 \pm 30$  and  $114 \pm 18$ ,

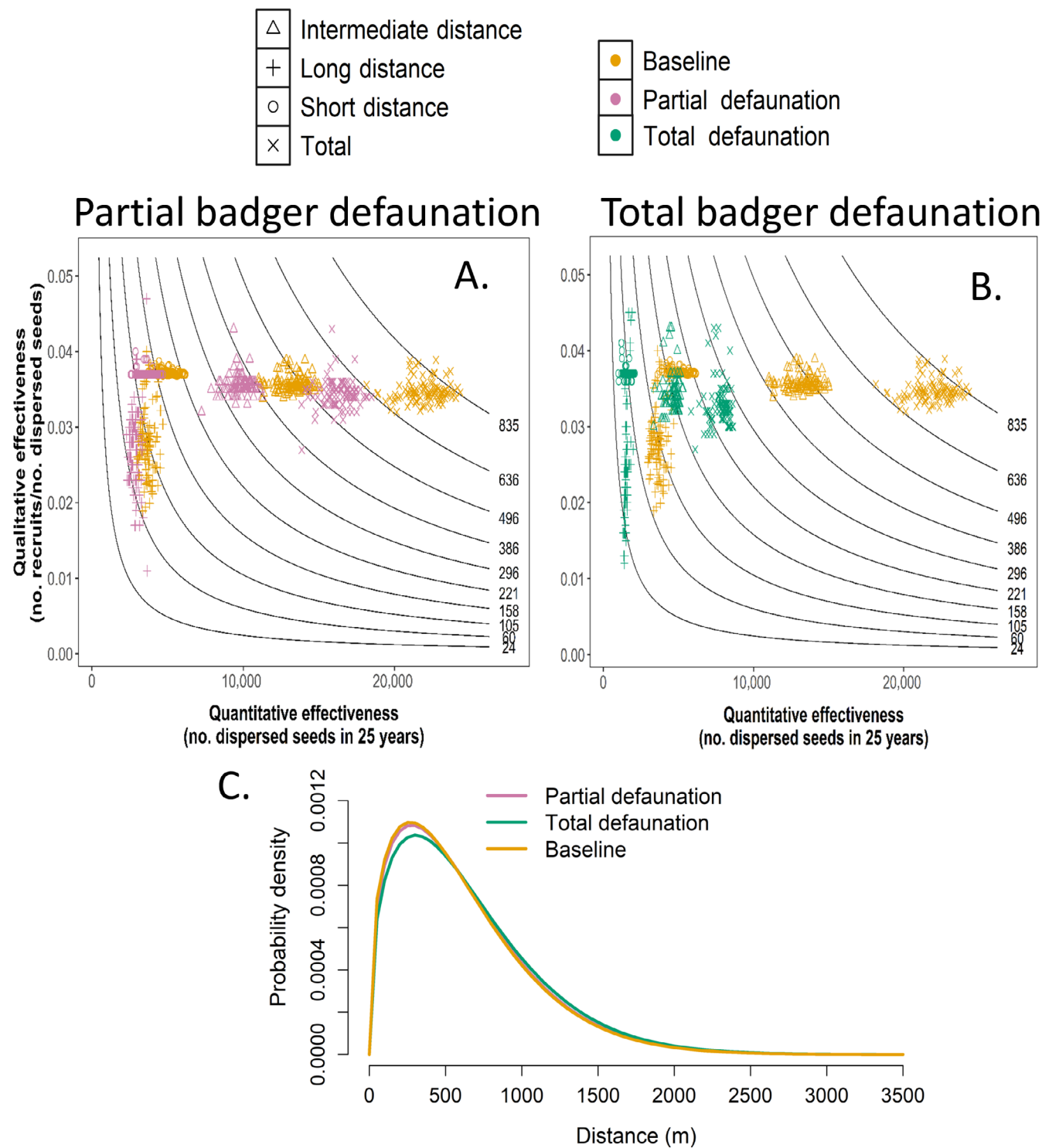
respectively) increased by 9% and 12% relative to the baseline value ( $102 \pm 21$ ), and (3) mild fragmentation did not noticeably change any aspect (quantitative and qualitative) of SDE for total, short, and intermediate-distance dispersal. Additionally, fragmentation produced some changes in seed dispersal distributions (Figure 6C); for instance, severe fragmentation increased the proportion of long-distance dispersal events by 12% relative to the baseline value (Appendix S6: Figure S1B).



**FIGURE 6** Seed dispersal effectiveness landscapes under baseline, mild, and severe fragmentation (A, B). (C) Averaged seed dispersal kernels under baseline, mild, and severe fragmentation scenarios. Each point represents the seed dispersal effectiveness of one out of 100 simulations.

Defaunation had a strong and species-dependent effect on SDE (Figures 7A,B and 8A,B). Specifically (1) partial and total badger defaunation decreased overall SDE ( $560 \pm 45$  and  $256 \pm 27$ , respectively) by an average

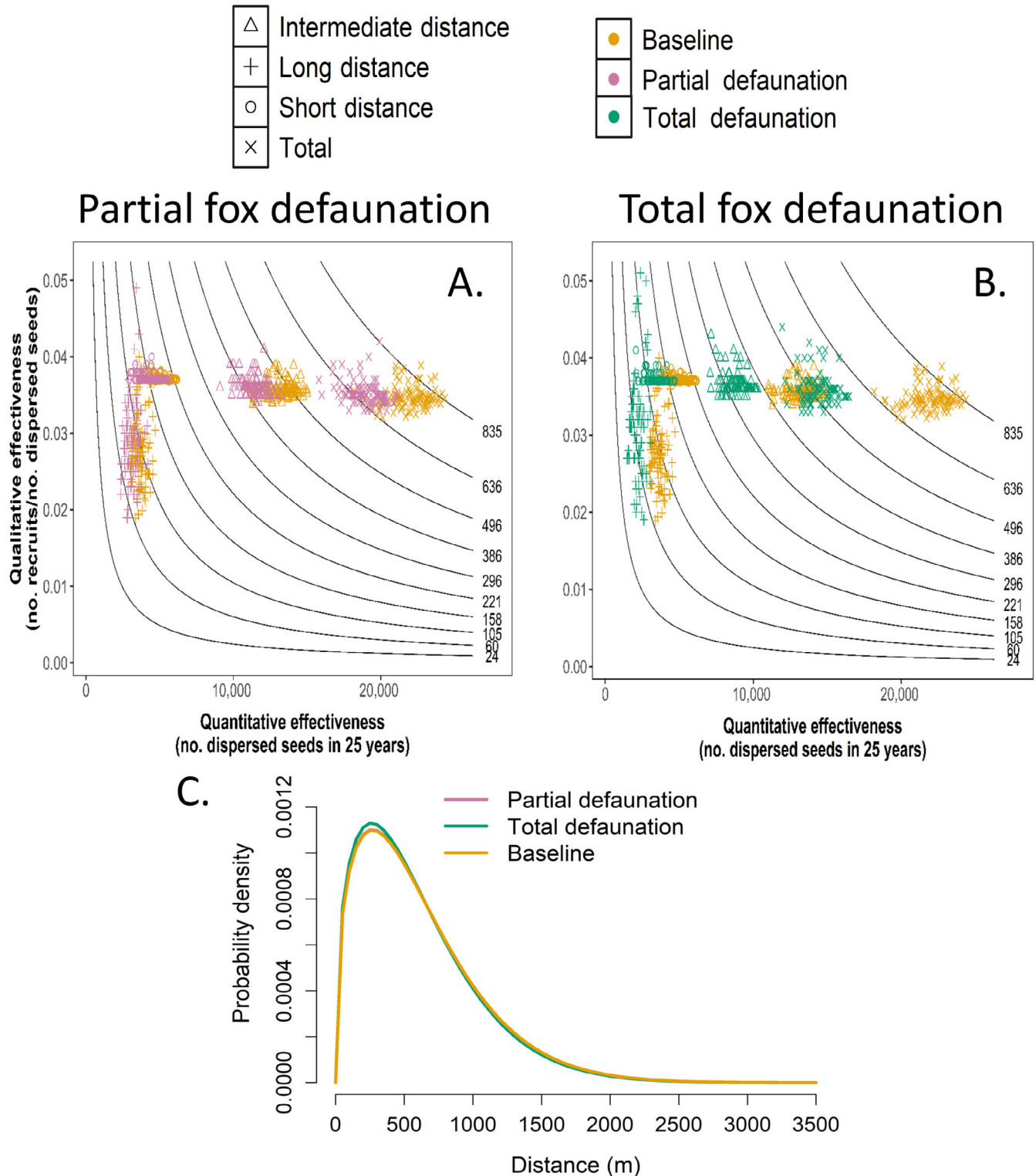
of 27% and 66%, whereas partial and total fox defaunation decreased overall SDE ( $667 \pm 42$  and  $520 \pm 40$ , respectively) by an average of 13% and 32% (relative to the mean baseline value:  $763 \pm 56$ ); these



**FIGURE 7** Seed dispersal effectiveness landscapes under baseline, partial, and total Eurasian *Meles meles* badger defaunation scenarios (A, B). (C) Averaged seed dispersal kernels under baseline, partial, and total badger defaunation scenarios. Each point represents the seed dispersal effectiveness of one out of 100 simulations.

negative impacts were of similar magnitude across spatial scales and mostly due to marked reductions in the quantitative component, (2) in general, neither badger nor fox defaunation had a noticeable impact on the qualitative

component. However, (3) badger and fox total defaunation ( $0.024 \pm 0.006$  and  $0.031 \pm 0.006$ , respectively) either slightly decreased or increased the qualitative component of long-distance dispersal relative to the



**FIGURE 8** Seed dispersal effectiveness landscapes under baseline, partial, and total red fox *Vulpes vulpes* defaunation scenarios (A, B). (C) Averaged seed dispersal kernels under baseline, partial, and total fox defaunation scenarios. Each point represents the seed dispersal effectiveness of one out of 100 simulations.

mean baseline value ( $0.028 \pm 0.004$ ). Finally, defaunation had a species-specific effect on seed dispersal distributions (Figures 7C and 8C). For example, the proportion of

long-distance dispersal increased by 17% under total badger but decreased by 8% under total fox defaunation (Appendix S6: Figure S1C,D).

## Combined effect of fragmentation and defaunation on SDE and dispersal kernels

The effects of landscape fragmentation and defaunation on the quantitative and qualitative components, and on overall SDE, were consistently additive (i.e., no evidence of interacting effects; see Appendix S7 for details).

## DISCUSSION

By combining long-term field data and spatially explicit individual-based modeling, we quantify, for the first time, the isolated and compounding impact of landscape fragmentation and defaunation on the quantity, quality, and overall SDE. Our results indicate that these two global change drivers generally limited seed dispersal and recruitment of a mammal-dispersed tree. Nonetheless, the magnitude and even the sign of the reported impacts on seed dispersal and recruitment varied with the spatial scale and species of seed disperser. In particular, under scenarios of strong perturbations, selection on long-distance seed dispersal could be either enhanced or weakened in the long term, altering in contrasting ways the ability of plants to cope with climate change (Fricke et al., 2022).

### The impact of landscape fragmentation and defaunation on SDE depended on the spatial scale and defaunated species

Fragmentation per se can have either a negative or a positive effect on biodiversity (Fahrig, 2017), but little is known concerning fragmentation effects on ecosystem functioning in general, and on seed dispersal in particular (Cazetta & Fahrig, 2022). Under baseline fragmentation, availability of the most unsuitable habitat (marshes) was much further away than near fruiting *P. bourgaeana* trees; thus, the proportion of seed dispersal events arriving into unsuitable marshes was orders of magnitude higher for long-distance than for short- and intermediate-distance seed dispersal. Such costs of seed dispersal, in terms of seed arrival into unsuitable habitats, augmented under scenarios of increased fragmentation for short- and intermediate-distance seed dispersal. Thus, our results indicated that fragmentation could put at risk the persistence of local populations, especially when fragmentation is relatively fine-grained (i.e., severe). Intriguingly, however, fragmentation increased (up to 12%) overall SDE of long-distance seed dispersal, which likely increase gene flow and connection among tree subpopulations (Emer et al., 2018;

Markl et al., 2012). Neither previous field (Cazetta & Fahrig, 2022) nor modeling (Chetcuti et al., 2021; Thierry et al., 2022) studies on fragmentation impacts have evaluated its consequences for plant recruitment. Though the strength of effect size was sometimes low, this study is novel in showing that the sign and the magnitude of the effect of fragmentation on plant recruitment (i.e., overall SDE) change with the spatial scale of concern.

Badger and fox defaunation markedly decreased the quantity of seed dispersal (Fedriani et al., 2020), with such an effect being relatively similar across spatial scales. Interestingly, here we show that whereas red fox defaunation caused an increase in the quality of long-distance seed dispersal, badger defaunation decreased it. Our study thus reveals that the effect of defaunation on SDE can be not only species-specific (Fontúrbel et al., 2015) but also scale-dependent. This is a key consideration both for a comprehensive understanding of the dynamic of plant metapopulations and for their appropriate management and restoration in human-impacted landscapes (see below). Finally, in our simulations, the effects of fragmentation and defaunation on SDE did not interact with each other. Additivity of multiple perturbation effects should lead to reduced cumulative impact on ecosystem functioning compared with synergistic interactions (Côté et al., 2016); therefore, from a conservation perspective, our result seems to give cause for cautious optimism (Brook et al., 2008; Darling & Côté, 2008).

### Impact of landscape fragmentation and defaunation on seed-dispersal distributions

Habitat fragmentation did not substantially change the overall number of dispersal events but altered the dispersal kernels by increasing the proportion of long-distance dispersal events. Given that the location of fruiting trees was held constant in our simulations, this result can be safely linked to changes in the distribution of marshes, open, and closed habitats where dispersers most often foraged, rested, and defecated (Fedriani et al., 1999). The increase in long-distance seed dispersal will likely have positive consequences for the tree meta-population dynamics, which is supported by the fact that landscape fragmentation also increased overall SDE. In the long term, higher and more effective long-distance dispersal would increase gene flow, connection among subpopulation, and colonization of vacant suitable habitats (Nathan et al., 2008; Spiegel & Nathan, 2007). Defaunation of both seed disperser species markedly decreased the number of dispersal events and overall SDE at all spatial scales. Further, red fox defaunation

decreased the relative number of long-distance dispersal events, which likely have mixed effects. On the one hand, it might negatively affect the tree dynamics at the whole meta-population scale (Nathan et al., 2008; Spiegel & Nathan, 2007). On the other hand, it can have a positive impact on local population dynamics by directing more of the dispersal events within the population rather than directing them to other populations/subpopulations (Gilpin, 2012).

## Applied implications

Taking into account that recruitment of *P. bourgaeana* in Doñana was very infrequent even in the baseline scenario (without any additional perturbation), it seems safe to assert that the current situation of this population is suboptimal for its long-term persistence. Indeed, field studies have indicated that the population exhibits very limited reproduction and regeneration ability (Fedriani et al., 2019) and shows a marked left-skewed demographic structure, with most individuals in older age classes, few juveniles, and even fewer seedlings and saplings (Żywiec et al., 2017; the authors' unpublished data). Urgent restoration actions to increase seed dispersal, recruitment, and establishment of *P. bourgaeana* and other low-density tree populations are clearly needed (Fedriani et al., 2017, 2019), especially in the current scenario of global change and increased tree mortality (Lewis et al., 2015; Trumbore et al., 2015; authors' unpublished data).

Some of our results concern the discussion about conflicts between biodiversity conservation and commodity production. A framework has been proposed that distinguishes between the integration ("land sharing") and separation ("land sparing") of conservation and production (Fischer et al., 2014; Phalan et al., 2011). Because we assessed the effect of fragmentation per se (by keeping constant the surface allocated to each habitat of the landscape), our results are relevant for the conservation and restoration of functional landscapes in the context of the land sharing versus land sparing debate. Specifically, our simulations showed that fragmentation increased the intermix of suitable and unsuitable habitat patches which, in turn, led to a decline in tree recruitment. Thus, land sparing may be a most appropriate strategy in heterogeneous landscapes whenever seed dispersal and plant recruitment are priorities (e.g., Edwards et al., 2021). This is particularly relevant in the Doñana area, where a rapid and ongoing expansion of an economic model based on intensive agriculture is escalating habitat loss and fragmentation while disregarding the biocapacity of its ecosystems (Camacho et al., 2022; Gürden, 2018).

To conclude, both targeted perturbations had a generally negative impact on SDE and plant recruitment; however, fragmentation per se could increase the proportion and effectiveness of long-distance dispersal events. Global change drivers are known to reduce the quantity of seed dispersal (Dirzo et al., 2014; Fedriani et al., 2020); however, our investigation is pioneering in showing that global change may also alter seed dispersal quality. Other costs and benefits of seed dispersal (e.g., seed treatment, gene flow) should be considered in future across scale evaluations of the impact of global change drivers on plant dynamics. Also, since fragmentation can lead to differential defaunation across seed disperser groups (e.g., birds vs. mammals; Liu et al., 2019), studies on how mixed perturbations alter the dynamics of plants dispersed by diverse assemblages of seed dispersers are needed. We show that a widespread integration of dispersal distance into the SDE framework is critical to fully understand the diverse impacts that human activity inflicts on plant dynamics. In the long term, scenarios of strong perturbations could either select for or against long-distance seed dispersal, which likely will alter in contrasting ways the ability of plants to cope with climate change.

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## CONFLICT OF INTEREST STATEMENT


The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data and some code used are already published and publicly available, with those publications properly cited herein. *DisPear* software (Fedriani et al., 2022) is available at Figshare: [https://figshare.com/articles/software/DisPear\\_version\\_3\\_0/19493828](https://figshare.com/articles/software/DisPear_version_3_0/19493828).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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