

# Seed dispersal in heterogeneous landscapes: linking field observations with spatially explicit models

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1 **Abstract**

2 Seed dispersal by animals drives persistence and colonization of the majority of  
3 fleshy-fruited plants. Different factors have been identified as important in shaping  
4 patterns of seed deposition. These factors include habitat heterogeneity, movement  
5 patterns of frugivore species, and their feeding behavior. Most studies, however,  
6 have analysed the effect of one factor at the time, either with a modelling approach  
7 or from field observations. Here, we combine empirical data with spatially-explicit  
8 models to explore the contribution of habitat availability and patterns of frugivore  
9 post-feeding flight distances to the spatial patterns of seed dispersal.

10 We found that both factors, distance from the mother tree and microhabitat  
11 identity, were shaping those patterns. Our results show that seed dispersal is tremen-  
12 dously heterogeneous and complex in space. The observed seed shadow is not the  
13 result of a single process but instead an intricate combination of distance and habi-  
14 tat selection. We suggest that the apparent combination of processes results from  
15 the simultaneous effects of distinct functional groups of frugivores.

16 keywords: *Taxus baccata* L., plant-animal interaction, microhabitat selection, dispersal  
17 distance, Bayesian statistics

# 1 Introduction

2 The establishment of new individuals is a critical step in plant population dynamics.  
3 Indeed, the persistence of populations and the colonization of new patches are directly  
4 conditioned by seed dispersal. In a vast majority of fleshy-fruited plant species, seed  
5 dispersal requires the interaction with frugivorous animals (Herrera, 2002). Zoochory  
6 is advantageous for plants in many ways. Frugivores allow the colonization of distant  
7 patches (Nathan, 2006; Wotton and Kelly, 2012), escape from herbivores and pathogens  
8 (Rice, 2002), and drive gene flow (Godoy and Jordano, 2001; Grivet et al., 2005; Dyer,  
9 2007).

10 Due to their central role, mutualistic plant-frugivore interactions have received much  
11 attention. Empirical studies have shown that frugivores select among the available mi-  
12 crohabitats in the landscape (Schupp, 1993; Graham, 2001; Holbrook and Smith, 2000;  
13 Spiegel and Nathan, 2009), which translates into strongly non-random, spatially struc-  
14 tured, seed shadows (Fragoso, 1997; Jordano and Schupp, 2000; García et al., 2007a).  
15 Open habitats tend to be avoided by frugivores while conspecific or other fruiting trees  
16 are often preferred (Alcántara et al., 2000; Jordano et al., 2007; García et al., 2007b;  
17 Martínez et al., 2008; Clark et al., 2004). However, fruiting trees, conspecific or not, are  
18 not necessarily suitable sites for seed germination. They usually receive high seed densities  
19 (Jordano and Schupp, 2000; Martínez et al., 2008; Herrera and García, 2009; unpublished  
20 data) that are likely coupled to high predation rates (García et al., 2005). Moreover,  
21 density-dependent and maternal neighborhood effects (Janzen, 1970) potentially cancel  
22 positive effects of higher germination rates (Schupp and Fuentes, 1995; Calviño-Cancela,  
23 2007; Sanz et al., 2009). Although we have a good understanding of the role of frugivores  
24 in the arrival of the seeds in suitable [microhabitats](#) for germination and potential seedling

1 establishment (Cousens et al., 2008), our knowledge is still limited in terms of assessing  
2 the relative importance of different factors such as frugivores' movement patterns (Herrera  
3 and García, 2009, 2010), dispersal distance (Schurr et al., 2009), and habitat heterogeneity  
4 (García et al., 2009).

5 Collecting reliable empirical data to link frugivore behavior to seed dispersal patterns is  
6 a costly and difficult task (Carlo et al., 2007; Carlo and Morales, 2008). As a consequence,  
7 our understanding of the spatial component of seed dispersal at the population level  
8 remains poor and there is the need to develop and test mechanistic models of the process  
9 (Nathan and Muller-Landau, 2000; Carlo and Morales, 2008; Cousens et al., 2008; Côrtes  
10 and Uriarte, 2012). The bulk of theoretical studies have focused on resource-tracking  
11 behavior of frugivores (Lehouck et al., 2009; Carlo et al., 2007) or landscape characteristics  
12 (Morales and Carlo, 2006; Carlo and Morales, 2008, for spatial aggregation; Levey et al.,  
13 2008, for patch shapes).

14 Some studies have attempted to incorporate frugivores' preferences, although in a pre-  
15 liminary way. Russo et al. (2006) included resting sites as the only habitat preference in  
16 addition to resource tracking. However, empirical studies show that frugivores use the  
17 surrounding vegetation in a more complex way (Jordano and Schupp, 2000). Resource  
18 tracking is an important driver of frugivore movements at the regional and landscape scale  
19 (Kollmann, 2000), especially in landscapes where fruit resources are scarce or distributed  
20 in distant patches (Alcántara et al., 2000). Nonetheless, frugivore movements are influ-  
21 enced by other properties of the surrounding vegetation matrix (e.g., the presence of hubs,  
22 Carlo et al., 2007; isolated trees, Herrera and García, 2009).

23 A major measurable outcome of the seed dispersal process is the distance from the  
24 mother tree at which a seed is deposited. The probability density function of the location  
25 of seed deposition with respect to the source define the dispersal kernel of a population

1 (Nathan and Muller-Landau, 2000). For this reason, the dispersal kernel is also commonly  
2 used as a surrogate of seed deposition (Clark et al., 1999; Higgins and Cain, 2002; Spiegel  
3 and Nathan, 2009). Also, it might be shaped by the spatial availability of habitat and  
4 therefore highly context-dependent (Carlo, 2005; Schurr et al., 2008).

5 These previous studies have significantly advanced our understanding of specific mech-  
6 anisms. What is still missing, however, is the complete picture of the interaction between  
7 dispersal agent behavior, landscape features, and seed deposition patterns. Little previous  
8 work has explored whether it is the microhabitat type or the distance from the source  
9 tree that influences bird foraging behavior, and thus seed deposition (but see Alcántara  
10 et al., 2000; Jordano and Schupp, 2000; Herrera and García, 2010).

11 In this study, we focus on *Taxus baccata* L., a long-lived, slow-growing conifer, and its  
12 avian seed dispersers to explore the extent to which landscape features, by modulating  
13 bird foraging behavior, drive seed-shadow patterns. We build spatially explicit models,  
14 parameterized from our field study, to answer the following questions: i) Do observed flight  
15 distances explain the spatial patterns of the seed shadow? ii) Is microhabitat availability  
16 a good predictor of spatial seed-shadow patterns? and iii) Are observed seed-shadows  
17 produced by a combination of distance and microhabitat availability? And if so, to what  
18 extent does each factor contribute to that spatial pattern?

## 19 **Material and methods**

### 20 **Species and study site**

21 The evergreen, non-resinous gymnosperm *Taxus baccata* L., the common yew, is a dioe-  
22 cious wind-pollinated tree (Thomas and Polwart, 2003; Sanz et al., 2009). It grows as  
23 an isolated or secondary forest tree from Norway to Northern Morocco. Embryos are  
24 protected by pseudobayes composed of a seed partially covered by a red and fleshy aril.

1 Hereafter, for simplicity, we will just use the term fruit. The common yew relies princi-  
2 pally on avian frugivores, especially *Turdus* spp. (Snow and Snow, 1988), for the dispersal  
3 of its seeds. By removing the surrounding aril, birds prevent fungal infection of the seeds  
4 and enhance seed germination (Heit, 1969; Fricke et al., 2013). Through their feeding  
5 behavior, birds set up the template for common yew population dynamics (Schupp and  
6 Fuentes, 1995).

7 The field study was conducted over two fruiting seasons, from August 2006 through  
8 December 2007, at the Barrerón de Escobarejos field site in the Sierra de Gredos, Spain  
9 (40°12'N, 5°60'W, elevation ranges from 1300m a.s.l. to 1400m a.s.l.). The studied  
10 population grows under a continental Mediterranean climate in the southern limits of  
11 its geographical range. It is located in the upper limit of a semideciduous oak forest  
12 (*Quercus pyrenaica*) on a north-facing slope and extended over 13ha. It comprised 21  
13 adult trees, 15 females and 6 males, distributed along seasonal streams surrounded by  
14 [shrublands](#). Vegetation is dominated by tall and medium-sized shrubs, mainly *Erica*  
15 *australis*, *E. arborea*, *Genista florida* and *Cytisus oromediterraneus*, with a few spatially-  
16 aggregated trees that produce fleshy fruits (*Sorbus aucuparia*, *Ilex aquifolium* and *Taxus*  
17 *baccata* L.) and non-fleshy fruits (*Quercus pyrenaica* and *Alnus glutinosa*). The highly  
18 fragmented landscape presents a rich mosaic of habitats at the local scale. Since the  
19 common yew is the dominant species at this site, and its disperser community is small,  
20 the local landscape configuration provides an adequate system to study seed dispersal in  
21 heterogeneous conditions.

## 22 **Seed sampling and feeding observations**

23 We defined six different types of microhabitats based on both soil type and vegetation  
24 cover: (1) “*T. baccata* female,” beneath a female conspecific tree; (2) “shrubs,” plant

1 species <1.50m in height; (3) “fleshy-fruited trees,” beneath trees other than the common  
2 yew that produce fleshy fruits and were >1.50m in height; (4) “non-fleshy-fruited trees,”  
3 beneath trees that do not produce fleshy fruits and were >1.50m in height; (5) “open  
4 ground,” deep soil with thick vegetation cover (pasture) or with gravel under 25cm<sup>2</sup>; (6)  
5 “rocks,” including stones on soil, boulders, and rock substrates of at least 25cm<sup>2</sup>. We  
6 categorized types 1–4 as “covered” microhabitats and types 5–6 as “open” microhabitats.

7 We quantified the seedfall patterns via a stratified sampling by microhabitat. Because  
8 of the presence of cattle and the absence of a fence in the study site, we used open  
9 quadrats of 0.5m × 0.5m instead of seed traps albeit they might be prone to seed losses.  
10 A study by Sanz and Pulido (2013) in the same location showed that seed predation by  
11 rodents was overall homogenous between microhabitats (see also Matías et al., 2009, for  
12 similar results). Also, Wang et al. (2012) showed that the seeds of [three of four studied](#)  
13 tree species were eaten and left *in situ*. Although our sampling method might not have  
14 prevented seed losses, [these](#) previous studies demonstrate that, when they happened,  
15 they were likely of similar magnitude in all open-quadrats. In addition, various studies  
16 have shown that this sampling method [provides reliable](#) estimates of the amount of seeds  
17 dispersed (Martínez, 2007; Carlo et al., 2013; García et al., 2005, 2011).

18 The sampling scheme consisted of an even number of sampling points per microhab-  
19 itat (when not constrained by microhabitat availability), each one being composed of  
20 two open quadrats located at a maximum distance of 0.5m from each other. Hereafter  
21 and for simplicity, we will refer to each sampling point as a seed-plot. Seed-plots were  
22 checked every two weeks for the identification and count of fallen seeds. We were able  
23 to distinguish between dispersed seeds—smooth seeds without aril—and non-dispersed  
24 seeds—those with aril. To account for post-dispersal predation, seeds collected inside  
25 the seed-plots and showing signs of rodent predation were counted as part of the pool of

1 dispersed seeds.

2 The female trees were unlikely to contribute equally to the overall seed rain of the  
3 study population. Existing studies have rather shown that bird visitation rates were  
4 correlated to fruit production (Blendinger et al., 2008; Vergara et al., 2010), therefore  
5 implying an heterogeneous contribution of individual mother trees. During the second  
6 fruiting season, in 2007, we estimated crop sizes by direct counts for all 15 female trees  
7 after all fruits had ripened, by late September. We counted the number of fruits left on  
8 the tree and removed by frugivores (by counting pedunculs) to estimate the total fruit  
9 yield. Depending on the size of the tree, we counted fruits in one quarter up to the  
10 entire canopy and multiplied accordingly to estimate the total crop size. Also, in both  
11 seasons studied, we counted the ripe fruits that had fallen underneath *T. baccata* female  
12 trees within the corresponding seed-plots. In 2007, the number of fruits fallen beneath  
13 a female tree was positively correlated with its fruit yield ( $R^2 = 0.7774$ ,  $P < 0.001$ ).  
14 Based on the positive correlation found in 2007 between crop sizes and fallen fruits, we  
15 summed, for each female tree, the number of fallen fruits collected over the two years  
16 of study. From this value,  $F_i$ , we calculated the probability of being visited by birds, a  
17 surrogate of individual contribution to the total seed rain, for each mother tree (see the  
18 “Spatially-explicit models” section).

19 We conducted direct feeding observations on a total of 11 female trees (of the 15 total)  
20 over the two years of study; the remaining female trees did not produce fruits. Two-hour  
21 observation sessions were performed during the activity range of frugivores (8:30–10:30,  
22 10:30–12:30 and 12:30–14:30) such that each tree was observed at least once during each  
23 period of time, for a total of 54 hours. During the observation sessions, we paid special  
24 attention to the bird’s behavior and recorded the following data for each bird sighted  
25 whenever possible: (1) bird species; (2) total time spent at the tree; (3) number of fruits

1 swallowed, if any; (4) exit flight distance; and (5) identity of first perch after leaving  
2 the focal tree. We followed each individual bird from the moment it entered the focal  
3 tree until it stopped on a first perch or until it was out of view. Because the study site  
4 is dominated by small shrubs, we had a good visibility to determine the identity of the  
5 first perch after a bird had left a *Taxus* tree. The flight distances to the first perch were  
6 estimated visually and validated a posteriori.

7 Prior to bird observations all seed-plots and trees in the study population were mapped  
8 (see the “Landscape structure” section for a description of the methodology). When flights  
9 were recorded between any two georeferenced points, we compared afterwards the value  
10 estimated from direct observation with the actual euclidean distance. Moreover, to avoid  
11 distance estimates biased towards short distances, we accounted for birds that flew out of  
12 view ; these observations represented 9% of all the recorded distances. When in the field,  
13 we estimated that these birds had flown a minimum distance of 100m. We thus, picked  
14 a random distance between 100m and 350m (see Martínez et al., 2008 and Godoy and  
15 Jordano, 2001, for dispersal kernels estimates of a similar assemblage of species).

## 16 **Landscape structure**

17 Each *T. baccata* tree and seed-plot in our study site was georeferenced using a Leica  
18 GS20 differential GPS. Post-processing using Leica GisDataPro software allowed for an  
19 average precision of 0.5m. Original data in geographic coordinates were projected in UTM  
20 coordinates using Quantum GIS 1.0.2 Kore software.

21 Virtual boundaries were set on the landscape based on the aerial photograph of the  
22 study site such that all *T. baccata* trees and seed-plots were included. The resulting spatial  
23 lattice covered a 260m × 510m area and was divided into 10m × 10m cells. Specifically,  
24 we located the seed-plots—for which we characterized the microhabitat in the field—on

1 the aerial photograph and visually classified the microhabitat types using those seed-plots  
2 as a reference. Based on the criteria established, we identified on the aerial photograph  
3 the microhabitats present in each cell of the lattice. We chose 100m<sup>2</sup> as the size of the cells  
4 because it is small enough to reflect most of the microhabitat variability in our landscape.  
5 Nonetheless, it is still too large to systematically assign a single microhabitat to each  
6 cell. Therefore, cells were classified in terms of the relative proportion of the different  
7 microhabitats they contain. We will refer to the microhabitat composition of a cell as its  
8 microhabitat vector. The spatial lattice was also projected in UTM coordinates so that  
9 we knew which *T. baccata* trees and seed-plots were found within each cell.

## 10 **Spatially-explicit models**

11 We sought to compare the amount of seeds observed at the seed-plot level with simulated  
12 data to understand the processes that drive seed deposition and the potential spatial  
13 interplay between them. To do so, we built three models that simulated seed dispersal.

14 The first and second model simulated distance-based and habitat-based seed dispersal,  
15 respectively, while the third was a combination of both distance and habitat. All models  
16 were parametrized with the spatial information defined in the previous sub-sections: the  
17 spatial position and microhabitat vector of each lattice cell, the distribution of *T. baccata*  
18 trees, and the seed-plot locations. [Fruit production,  \$F\_i\$ , was assigned to individual female](#)  
19 [trees as explained previously.](#)

### 20 **Distance-based model**

21 In the first model, based on distance, the arrival of a seed to a cell is determined by the  
22 seed-dispersal kernel. We approximated the dispersal kernel with a Weibull distribution  
23 with best-fit parameters estimated from empirically-observed flight distances (Fig. 1b).

1 Since every flight was a random observation of full foraging sequence, we assume that  
2 unique flight distance data provide us with a reliable estimate of the distribution of flight  
3 distances. By doing so we did not account for the gut passage time of the different bird  
4 species involved in the dispersal of the seeds. However, these birds frequently regurgi-  
5 tate rather than defecate the seeds thus resulting in short time interval between feeding  
6 and dispersal events (Sorensen, 1984; Jordano and Schupp, 2000). Moreover, our fitted  
7 Weibull distribution is consistent with the fat-tailed kernels typically found in the lit-  
8 erature (Jordano and Schupp, 2000; Grivet et al., 2005; García et al., 2007a; Martínez  
9 et al., 2008). Finally and most importantly, two studies conducted in southern Spain, at  
10 the same study site, found similar seed dispersal kernels using either field observations  
11 (Jordano and Schupp, 2000) or molecular techniques (Godoy and Jordano, 2001).

12 In this model, a female tree is first selected according to its fruit production as follows:

$$a_i = \frac{F_i}{\sum_{j=1}^T F_j}, \quad (1)$$

13 where  $a_i$  is the probability of selecting mother tree  $i$ ,  $F_i$  is its fruit production, and  
14 the sum is over all  $T$  mother trees. Next, the dispersal direction was picked uniformly at  
15 random and the dispersal distance was randomly selected from the parameterized Weibull  
16 distribution. Given the distance and direction, we directly determined in which cell the  
17 seed falls. In the event that the seed falls outside the boundaries of the landscape, we  
18 ignore it and disperse a new seed. In addition, to measure seed dispersal at the seed-plot  
19 scale, we use the probability  $p_{st}$  that a seed, once falling in a cell, landed in a seed-plot:

$$p_{st} = \frac{N_t A_t}{A_c}, \quad (2)$$

20 where  $N_t$  is the number of seed-plots within the cell,  $A_t$  is the area of a seed-plot (0.5m<sup>2</sup>),

1 and  $A_c$  is the total area of the cell (100m<sup>2</sup>). The simulation stopped when the sum of the  
 2 number of simulated seeds in the seed-plots equaled 5398, the total number of dispersed  
 3 seeds collected in our experiment over the two years studied.

#### 4 **Habitat-based model**

5 In the second model, based on habitat selection, the arrival of a seed is determined by the  
 6 microhabitat type and its proportion within a cell. In this model, we used the pattern of  
 7 microhabitat selection by frugivores as a surrogate for seed deposition patterns (Fig. 1c).  
 8 Therefore, we estimated the proportion of flights to each microhabitat type directly from  
 9 field data and incorporated these proportions in the model. We first selected a tree  
 10 according to its fruit production from Eq. 1, just as above. Next, a microhabitat is picked  
 11 based on birds' selection:

$$h_i = \frac{P_i}{\sum_{j=1}^H P_j}, \quad (3)$$

12 where  $h_i$  is the probability of selecting microhabitat  $i$ ,  $P_i$  is the observed number of flights  
 13 to microhabitat  $i$ , and the sum is over all  $H$  microhabitats. From the subset of cells where  
 14 the selected microhabitat is present, we chose one cell according to the fraction of that  
 15 microhabitat that it contains. In doing so, we take into account that larger microhabitat  
 16 patches will attract bird species more often. Finally, the probability  $p_{st}^h$  for a seed to fall  
 17 both into a cell and into a seed-plot is given by:

$$p_{st}^h = \frac{N_t^h A_t}{P_h A_c}, \quad (4)$$

18 where  $p_{st}^h$  is the probability for a seed to be dispersed into a seed-plot of a particular  
 19 microhabitat within a cell,  $N_t^h$  is the number of seed-plots in that particular microhabitat

1 within that cell, and  $P_h$  is the proportion of the microhabitat within the cell. As before,  
2  $A_t$  is the area of a seed-plot ( $0.5\text{m}^2$ ), and  $A_c$  is the total area of the cell ( $100\text{m}^2$ ). Again,  
3 the simulation stopped when the sum of the number of simulated seeds in the seed-plots  
4 equaled 5398, the observed number of dispersed seeds.

### 5 **Distance- and habitat-based model**

6 In the third model, we combine the two previous models so that a seed falls into a cell  
7 depending on both the microhabitat type available and the distance from the female  
8 tree. To explicitly account for the interaction between microhabitat and distance, we  
9 estimate the microhabitat-specific seed-dispersal kernels from the corresponding subsets  
10 of exit flight distances. The microhabitats for which the seed-dispersal kernels were not  
11 statistically different were grouped (group1: open ground, rocks, and non-fleshy-fruited  
12 trees; group2: fleshy-fruited trees and shrubs; group3: *T. baccata* female trees).

13 In this model, a female tree is first picked according to its fruit production from  
14 Eq. 1 and a microhabitat is selected according to bird's selection from Eq. 3. Once the  
15 microhabitat is chosen, a distance is picked from the seed-dispersal kernel specific of that  
16 microhabitat. The cell where the seed will land is chosen from the cells containing the  
17 selected microhabitat and located at the selected distance. In the first two models, a seed  
18 was dispersed according to the distance from the source tree or the microhabitat type,  
19 whereas in this third model the two components are explicitly combined. The probability  
20 for a seed to land into both a cell and a seed-plot is calculated as in Eq. 4. As for the  
21 two previous models, the simulation stopped when the sum of the number of simulated  
22 seeds in the seed-plots equaled 5398, the observed number of dispersed seeds. Hereafter,  
23 this model will be referred to as the interaction model for simplicity.

## 1 Data analyses

2 We ran 10,000 replicates of each model and recorded the number of seeds per cell and per  
3 seed-plot for each replicate. For each model replicate, we compared the simulated number  
4 of seeds-per-seed-plot with the empirical number of seeds following:

$$D_{obs} = \sum_{i=1}^n (O_i - \bar{E}_i)^2, \quad (5)$$

5 where  $i$  is the seed-plot,  $O_i$  is the empirical number of seeds per seed-plot,  $\bar{E}_i$  is the  
6 mean simulated number of seeds per seed-plot, and the sum is over all  $n$  seed-plots. We  
7 then calculated  $D_{exp}$  in a similar manner than in Eq. 5. That is, we used the simulated  
8 number of seeds of a replicate instead of the empirical number of seeds per seed-plot in  
9 our calculation. This procedure was repeated for each simulated replicate to obtain a  
10 distribution of  $D_{exp}$  values. If a model explains the observed data, the value  $D_{obs}$  would  
11 fall within the 95% confidence interval of the  $D_{exp}$  distribution (D’Agostino and Stephens,  
12 1986).

13 In addition, to estimate the overall fit of the model as described above, we quantified  
14 the goodness-of-fit on a seed-plot basis to account for the potential spatial heterogeneity  
15 in the prediction of the models. The probability of reproducing the empirical data at the  
16 seed-plot scale was given by:

$$p_i = \frac{N_i^{obs}}{N_{sim}}, \quad (6)$$

17 where  $p_i$  is the probability of obtaining the empirical value among the simulated values  
18 for seed-plot  $i$ ,  $N_i^{obs}$  is the number of times that the simulated value equals the observed  
19 value for seed-plot  $i$ , and  $N_{sim}$  is the total number of simulated replicates. The model that  
20 has the highest probability best explained the observed value at that particular seed-plot

1 compared to the other two models.

2 We used a nested-sampling algorithm to estimate the relative contribution of each  
3 process to the overall seed shadow (Sivia and Skilling, 2006). To do so, we first made use  
4 of the likelihood of any candidate model  $M$  defined as:

$$L(M) = \prod_{i=1}^n p_i^M, \quad (7)$$

5 where  $L(M)$  is the likelihood of model  $M$  and  $p_i^M$  is the probability of reproducing the  
6 empirical data within seed-plot  $i$  (calculated as in Eq. 6) for model  $M$ . In the nested-  
7 sampling procedure, we simulated seed dispersal anew but, instead of running a single  
8 model many times, we selected a different seed-dispersal rule for each seed (i.e., dispersal  
9 based on distance-only, microhabitat-only, or both). The algorithm starts with arbitrary  
10 initial probabilities assigned to the three models. Under such a model, a seed-dispersal  
11 rule is first picked according to its probability and the seed dispersed according to the  
12 corresponding model. The nested-sampling algorithm then explores the space of possible  
13 combinations while attempting to maximize the likelihood. As a result, we are able  
14 to directly estimate the optimal combination of the three dispersal mechanisms at the  
15 seed-scale as well as obtain Bayesian estimates of the confidence intervals around this  
16 combination.

## 17 Results

### 18 Field data

19 Based on the microhabitat vector assigned to each cell of the spatial lattice, we estimated  
20 the availability of each microhabitat type. The landscape was dominated by open areas  
21 (open ground: 40.5%; rocks: 9.4%) and low shrubs (43.3%). Trees represented just 7%

1 of the study site (non-fleshy fruited trees: 6.2%; fleshy-fruited trees: 0.2%; *T. baccata*  
2 female trees 0.4%)

3 The frugivore guild associated with the common yew in the study population was  
4 composed of a few species. Three bird species fed most frequently on *T. baccata* trees  
5 (Table 1): Blackbirds (*Turdus merula*), Mistle Thrushes (*T. viscivorus*), and Blackcaps  
6 (*Sylvia atricapilla*). Ring Ouzels (*T. torquatus*) and Eurasian Jays (*Garrulus glandarius*)  
7 were observed only occasionally and their contribution to the seed shadow is likely to be  
8 marginal. One seed predator, the Great Tit (*Parus major*), was present, although it only  
9 damages a small fraction of fruits (Table 1).

10 Individuals of *T. viscivorus* consumed the highest mean number of fruits, followed  
11 by *T. merula* and *S. atricapilla* (Table 1). However, since only a few individuals of  
12 *T. viscivorus* and *S. atricapilla* were observed feeding on *T. baccata* trees, 13 and four  
13 respectively, most of the seeds were dispersed by *T. merula*. All of the species spent  
14 substantial time perching per visit in yew trees and showed high variability in the mean  
15 number of fruits consumed per individual. With the exception of *T. viscivorus*, that was  
16 absent in 2006, all other species were present in both years. Despite some differences  
17 in species traits (e.g., meal size, flight distances), we considered the frugivore guild as a  
18 whole in order to increase the size of our dataset. Analyses were therefore conducted at  
19 the guild level.

20 During the two years of study, a total of 337 exit flights were recorded from direct  
21 bird observations. Slightly more than 50% of those flights were consecutive to a feeding  
22 event. From those, 89% were from *Turdus merula*. Typically, *Turdus merula* individuals  
23 were observed feeding on a *Taxus* tree, then flying to a close tree and flying back to  
24 the first *Taxus* tree, thus remaining in the vicinity of the source tree for a substantial  
25 amount of time (personal observation). The foraging behavior of *T. merula* coupled with

1 short regurgitation times (Sorensen, 1984) lead to a high probability of seed deposition  
2 under the source tree or in its immediate vicinity. Indeed, the resulting flight distances  
3 distribution was strongly skewed towards short distances (Jordano and Schupp, 2000;  
4 Martínez et al., 2008). We fitted flight distances data to a Weibull distribution (global  
5 seed-dispersal kernel: scale = 24.75 and shape = 0.843, Fig. 1b; group1 seed-dispersal  
6 kernel: scale = 17.09 and shape = 0.829; group2 seed-dispersal kernel: scale = 28.81 and  
7 shape = 1.072; group3 seed-dispersal kernel: scale = 6.92 and shape = 2.029).

8 A total of 93.3% of the exit flights were to microhabitats with vegetation cover. We an-  
9 alyzed the frequencies in a number-of-flights  $\times$  microhabitat contingency table, controlling  
10 for microhabitat availability, to assess selection patterns in the choice of the first perch.  
11 We estimated the significance of individual residual frequencies with the chi-square distri-  
12 bution with the global degrees of freedom. The frugivore guild showed a marked tendency  
13 to use particular microhabitat types ( $\chi^2 = 1156$ ,  $df = 5$ ,  $P < 0.001$ , Fig. 1c), especially  
14 trees independent of whether they produce fleshy fruits (conspecific or not) or non-fleshy  
15 fruits.

## 16 Simulations

17 Each of the three models provided seed-dispersal simulations at the landscape and seed-  
18 plot scale. All three models produced distinct overall patterns of seed density (Fig. 2). In  
19 the distance-based model, most seeds were dispersed around the female trees, leading to  
20 a clumped seed shadow. The habitat-based generated a more homogeneous seed-shadow  
21 pattern since almost all of the cells received seeds, albeit in variable proportions. The  
22 interaction model produced a pattern that most closely resembles that of the distance-  
23 based model. Large areas of the landscape received low seed densities; however, the  
24 resulting seed shadow was less symmetric since it adjusted more to the shape of preferred

1 habitat patches.

2 The overall fit of each model to the empirical data was assessed based on the distance  
3  $D$  from Eq. 5. None of the three models was a strong predictor of the global distribution  
4 of the number of seeds per plot; that is, the probability of the models generating a similar  
5 seed shadow was very small ( $P < 0.001$  for all models). Nevertheless, since the models  
6 produced spatially-heterogeneous patterns, we checked for the goodness-of-fit on a seed-  
7 plot by seed-plot basis.

8 The probability to generate the empirical value was highly variable between seed-plots  
9 (Fig. 3). The habitat-based model in general performed rather poorly. It predicted the  
10 observed number of seeds with a probability of at least 0.5 in only 3% of the seed-plots.  
11 The distance-based and interaction models produced more similar results to each other. In  
12 the distance-based model, the empirical number of seeds was predicted with a probability  
13 of at least 0.5 and 0.8 in a larger fraction of seed-plots than in the interaction model (25%  
14 and 18%, respectively, for the distance-based model; 24% and 15% for the interaction  
15 model). At higher thresholds, however, the interaction model performed slightly better.  
16 It predicted the empirical number of seeds with a probability of at least 0.9 in 12% of the  
17 seed-plots while this proportion drops to 5% for the distance-based model. We identified  
18 the best individual model (i.e., the one with the highest probability) on a seed-plot basis  
19 (Fig. 4). Although a model was assigned to every seed-plot, this does not necessarily  
20 imply a good fit of that model. As before, the distance-based model has the highest  
21 number of seed-plots associated (45%). The habitat-based model is associated with 23%  
22 of the seed-plots and 32% are associated with the interaction-based model. The subsets of  
23 seed-plots best explained by each model did not display any clear spatial pattern (Fig. 4).

24 To that point, we implicitly assume that all the seeds within a seed-plot were dispersed  
25 by the same process (distance, habitat, or a combination of both). However, those seeds

1 may not necessarily have been dispersed by the same process which could explain the lack  
2 of concluding results in the previous analyses (Figs. 3 and 4). Using Eq. 7, we explored the  
3 combination of the three processes (distance, habitat, and interaction ) that would best fit  
4 the empirical data at the seed-level. The combination that maximizes the log-likelihood  
5 (i.e., that provides the best fit to the empirical data) was one in which 99% ( $\pm 0.4$ ) of the  
6 seeds were dispersed based on the interaction between distance and habitat, 1% ( $\pm 0.006$ )  
7 based on microhabitat selection and no seeds were dispersed based on distance alone.

## 8 **Discussion**

9 Seed dispersal is a spatially-complex and multi-agent process (Nathan and Muller-Landau,  
10 2000; Alcántara et al., 2000; Jordano et al., 2007). Understanding the contribution of the  
11 different agents involved and how they interact with the local spatial context is far from  
12 straightforward. Here, we have incorporated fine-scale, geographic information into mech-  
13 anistic seed dispersal models to disentangle the role of landscape features in determining  
14 seed fate. We successively tested the role of distance from the mother tree, the role of mi-  
15 crohabitat type and finally the role of the interaction between the two. The three models  
16 successively tested for increasing complexity in the potential mechanisms that generate  
17 seed-shadow patterns.

18 Overall, none of the models explained the empirical seed-shadow patterns demon-  
19 strably better than the others, despite the contrasting output they produced (Fig. 2).  
20 However, it is important to note that the lack of fit was not homogeneous across seed-  
21 plots (Fig. 3). The subset of seed-plots located on the west side and southeast corner of  
22 the landscape remained largely unexplained. In contrast, the subsets of seed-plots in the  
23 center and on the east side of the landscape were generally slightly better predicted by  
24 the distance-based model (Fig. 3).

1        Interestingly enough, the seed-plots that were best explained in all scenarii – in the  
2 center and east side – tended to be located at a considerable distance from the mother  
3 trees with the highest fruit production – on the west side (Figs. 1 and 3). In our field  
4 experiment, this subset of seed-plots received a small amount of seeds. Indeed, the dis-  
5 tance and interaction models adjusted well to those seed-plots, suggesting that they can  
6 predict where the seeds will not be dispersed in the landscape. Surprisingly, the habitat-  
7 based model performed rather poorly. Given the frugivorous birds’ avoidance of open  
8 habitats, pointed out in many studies (Alcántara et al., 2000; Jordano and Schupp, 2000;  
9 Bartuszevige and Gorchov, 2006; Martínez et al., 2008), we expected that at least the  
10 avoided habitat patches would be well-predicted by the model. The spatial patterns in  
11 the goodness-of-fit of the three models suggest that a simple process, such as distance,  
12 might explain low seed densities away from the source tree, while more complex processes  
13 might drive seed deposition at a local scale.

14        The nested-sampling analysis reveals that, in the best-fit scenario, 99% of the seeds  
15 were dispersed by a process resulting from the interaction between the distance from the  
16 source tree and the microhabitat type and, most interestingly, that no seeds were dispersed  
17 by a process involving distance alone. This analysis, at the seed-level, highlights that each  
18 seed within a landscape might be dispersed by a unique seed-specific dispersal process  
19 resulting from the interaction between maternal tree location, bird species’ identity, and  
20 microhabitat type.

21        The failure of the three models in predicting the spatial patterns of seed deposition  
22 could be a methodological bias. The method that we used to fit the observed flight  
23 distances might not have accurately estimated the true dispersal kernel (Robledo-Arnuncio  
24 and García, 2007). Nonetheless, as discussed previously, the models mostly failed to  
25 predict the number of dispersed seeds in the immediate vicinity of the female trees. This

1 suggests that, if distance was in fact the process driving seed deposition, we would have  
2 underestimated local dispersal. Although a finer estimate of the dispersal kernel could  
3 have quantitatively improved our results, they might have remained qualitatively similar.

4 A possible explanation of the apparent spatial asymmetry of the fit of the models could  
5 be the confounding effects of different functional groups of frugivores (Martínez et al.,  
6 2008). We can distinguish the behavior of *S. atricapilla* and *T. merula* on one hand, and  
7 *T. viscivorus* on the other. *Sylvia atricapilla* is an abundant and regular wintering species  
8 in Spain (Jordano and Herrera, 1981) while *T. merula* is a resident and territorial species  
9 (Greenwood and Harvey, 1978). Both species, however, display a similar movement range  
10 (mostly within 50m, personal observation) and short gut passage time (Jordano, 1987,  
11 for *S. atricapilla*, Sorensen, 1984, for *T. merula*). We rarely observed these species flying  
12 through open areas. They might thus contribute to the seed shadow in the immediate  
13 proximity of the female trees. Moreover, *T. merula* individuals prefer to remain beneath  
14 the canopy cover and use some trees as roosting sites; this likely translates into non-  
15 random, directed seed deposition.

16 *Turdus viscivorus*, on the other hand, is a migrant species. Although resident popu-  
17 lations were present in the area, we did not observe such population at our study site.  
18 Individuals typically fly much longer distances and preferentially select tall trees for perch-  
19 ing (Jordano and Schupp, 2000; Jordano et al., 2007). We frequently observed individuals  
20 flying out of view but rarely to the other side of the population (west side of the land-  
21 scape). Due to this asymmetric use of the landscape, *T. viscivorus* might have dispersed  
22 the seeds of only a subset of the female trees. Furthermore, *T. merula*, *S. atricapilla*, and  
23 *T. viscivorus* display distinct flight distance distributions (Jordano et al., 2007; Martínez  
24 et al., 2008). As a consequence, applying different dispersal kernels to individual mother  
25 trees, depending on the frugivore species that visit them, may possibly improve the fit of

1 our models to the observed data.

2 The models implicitly assume that microhabitat selection is the only factor caus-  
3 ing anisotropic movements of birds. Nevertheless, landscape elements such as isolated  
4 trees (Herrera and García, 2009), food resources (Graham, 2001) or topographic variation  
5 (Westcott, 1997) may also determine anisotropic movement patterns. The existence  
6 of preferred elements in the landscape for perching or feeding, also called hubs, is a  
7 probable cause of the variation in the goodness-of-fit at the seed-plot level (Carlo et al.,  
8 2007). Marked directionality, actually observed in the studied population (personal ob-  
9 servation), is likely to create a non-uniform seed deposition within the studied landscape  
10 (García et al., 2007a; Carlo et al., 2013).

11 In the studied population, yew female trees displayed highly heterogeneous crop sizes.  
12 Indeed, two female trees located in the central area of the landscape did not produce  
13 fruits at all over the two studied years (Fig. 1a), probably due to pollen limitation (Sanz,  
14 2008). From the frugivore's perspective, these two female trees are similar to the other non  
15 fleshy-fruited trees in the population. Indeed, because these female trees failed in acting  
16 as stepping stones (Herrera and García, 2009) and because there are no corridors (Levey  
17 et al., 2005), the east and west vegetation patches might not be functionally connected.  
18 In fact, birds are likely to forage within distinct vegetation patches and only rarely flew  
19 from one patch to the other (see Graham, 2001, for the cost-distance hypothesis). Our  
20 study site might not be a single population, but rather two patches displaying distinct  
21 seed dispersal dynamics.

22 In this study, we have developed a mechanistic spatially-explicit model to explore the  
23 seed-dispersal process in a real ecological context. The incorporation of spatial data high-  
24 lights the complexity of such a process. Despite the patterns that have emerged from theo-  
25 retical studies, predicting what actually happens in nature remains a difficult task. Nathan

1 and Muller-Landau (2000) highlighted the necessity for more studies testing “predictions  
2 based on disperser behavior against field data.” To our knowledge, studies integrating  
3 empirical data of frugivore movements and seed-shadow patterns with spatially-explicit  
4 mechanistic models are scarce (but see Levey et al., 2005, Morales et al., 2013). Although  
5 simple, these models are a first step towards a better understanding of the complexity of  
6 interactions taking place in natural ecosystems. This study underlines the crucial need  
7 for integrated approaches to unravel the role of frugivores in shaping spatial patterns of  
8 plant populations and to move from local to global scales.

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## Figure captions

**Figure 1:** Empirical observations used to parametrize the seed dispersal models. a) Aerial photograph of the study site showing the location of the *T. baccata* female trees. Circle size is proportional to the fruit production of each tree. [The dotted line represents the boundaries of the spatial lattice used in the three models.](#) b) Frequency distribution of flight distances collected from direct observation in the field. The data were fit to a Weibull distribution (solid line). c) Residuals of a contingency-table analysis of bird flights to microhabitat type, all species pooled. Individual bars represent residual frequencies and significant positive residuals indicate microhabitats favored while significant negative residuals indicate microhabitats avoided. \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ . R: rocks; G: open ground; S: shrubs; N: non fleshy-fruited trees (including *T. baccata* male trees); F: fleshy-fruited trees (excluding *T. baccata* female trees); TF: *T. baccata* female trees.

**Figure 2:** Simulated seed densities across the landscape for the three models described in the text. Each panel represents one realization of the model and the color of the cells indicates high (dark green) or low (white) seed density probability. The black dots show the location of the female trees within the landscape. a) Distance-based seed dispersal model; b) Habitat-based seed dispersal model; c) Distance- and habitat-based seed dispersal model. It is visually apparent that the different models lead to distinct seed shadows.

**Figure 3:** Model goodness-of-fit at the seed-plot level. Boxes represent the seed-plots of the field experiment and the colorbar corresponds to the probabilities that the model generates the observed number of seeds, among all simulated replicates (10,000). a) Distance-based seed dispersal model; b) Habitat-based seed dispersal model; c) Distance and habitat-based seed dispersal model. The different models are able to explain well distinct subsets of seed-plots.

**Figure 4:** Best-fit model on a seed-plot basis. Colors indicate the model with the highest probability of reproducing the observed number of seeds. Each model best predicts a comparable number of seed-plots. Interestingly, there is little apparent spatial organization of the model differences.

**Table 1:** Visit frequencies, meal size, and visit duration of main seed dispersers of *T. baccata*.

Bird species	Perching <sup>(1)</sup>	Handling fruits <sup>(2)</sup>	N fruits <sup>(3)</sup>	Visit duration <sup>(4)</sup>
Seed dispersers				
<i>Turdus merula</i>	0.62 (108)	0.87 (158)	3.66 ( $\pm$ 2.75)	2.0 [1.0–3.0]
<i>Turdus viscivorus</i>	0.04 (14)	0.07 (13)	5.50 ( $\pm$ 3.90)	5.0 [1.4–5.0]
<i>Sylvia atricapilla</i>	0.04 (5)	0.02 (4)	2.38 ( $\pm$ 1.03)	5.0 [1.3–5.0]
Other species <sup>†</sup>	0.02 (1)	0.01 (2)	0.75 ( $\pm$ 0.35)	–
Seed predator				
<i>Parus major</i>	0.28 (27)	0.03 (5)	1.10 ( $\pm$ 0.55)	1.0 [0.5–1.3]

<sup>1</sup>Relative visit frequencies to *T. baccata* trees without feeding and number of individuals (in parentheses).

<sup>2</sup>Relative visit frequencies to *T. baccata* trees with feeding and number of individuals (in parentheses).

<sup>3</sup>Number of fruits handled per visit and per individual (excluding individuals only perching), mean  $\pm$  1 SE (in parentheses)

<sup>4</sup>Mode [25–75% quantiles], time in minutes.

<sup>†</sup>*Garrulus glandarius* and *Turdus torquatus*

Figure 1

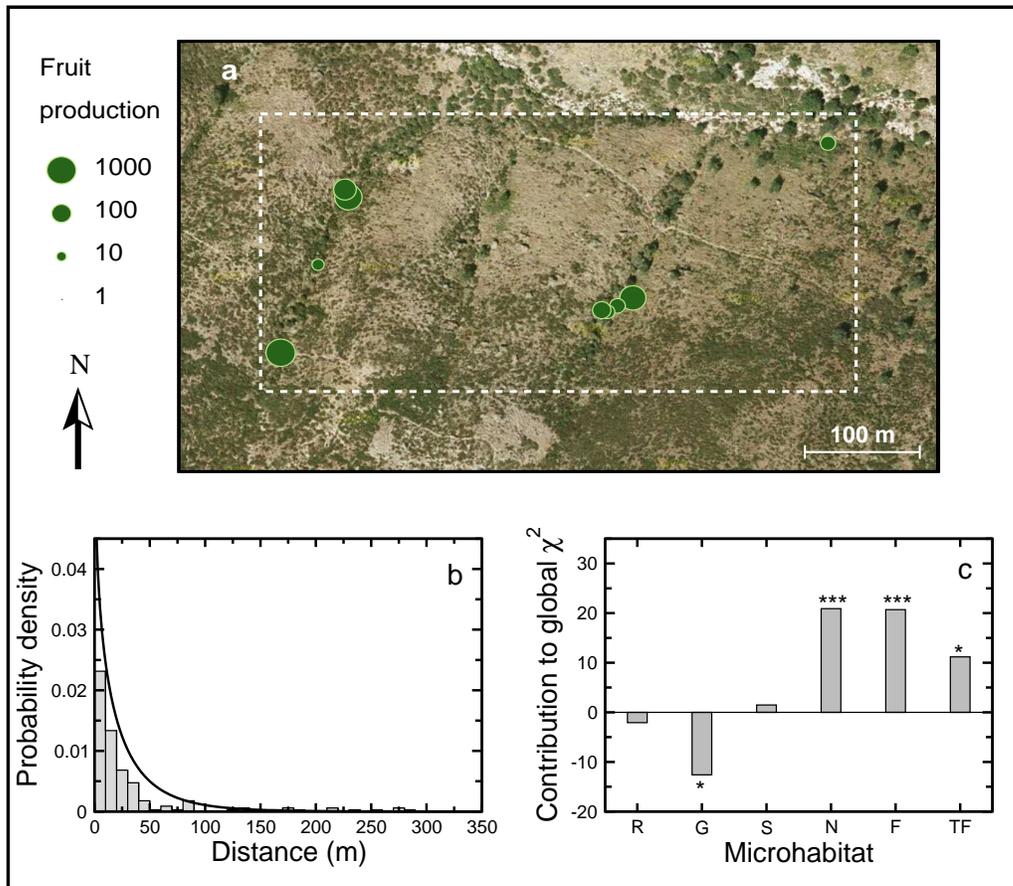


Figure 2

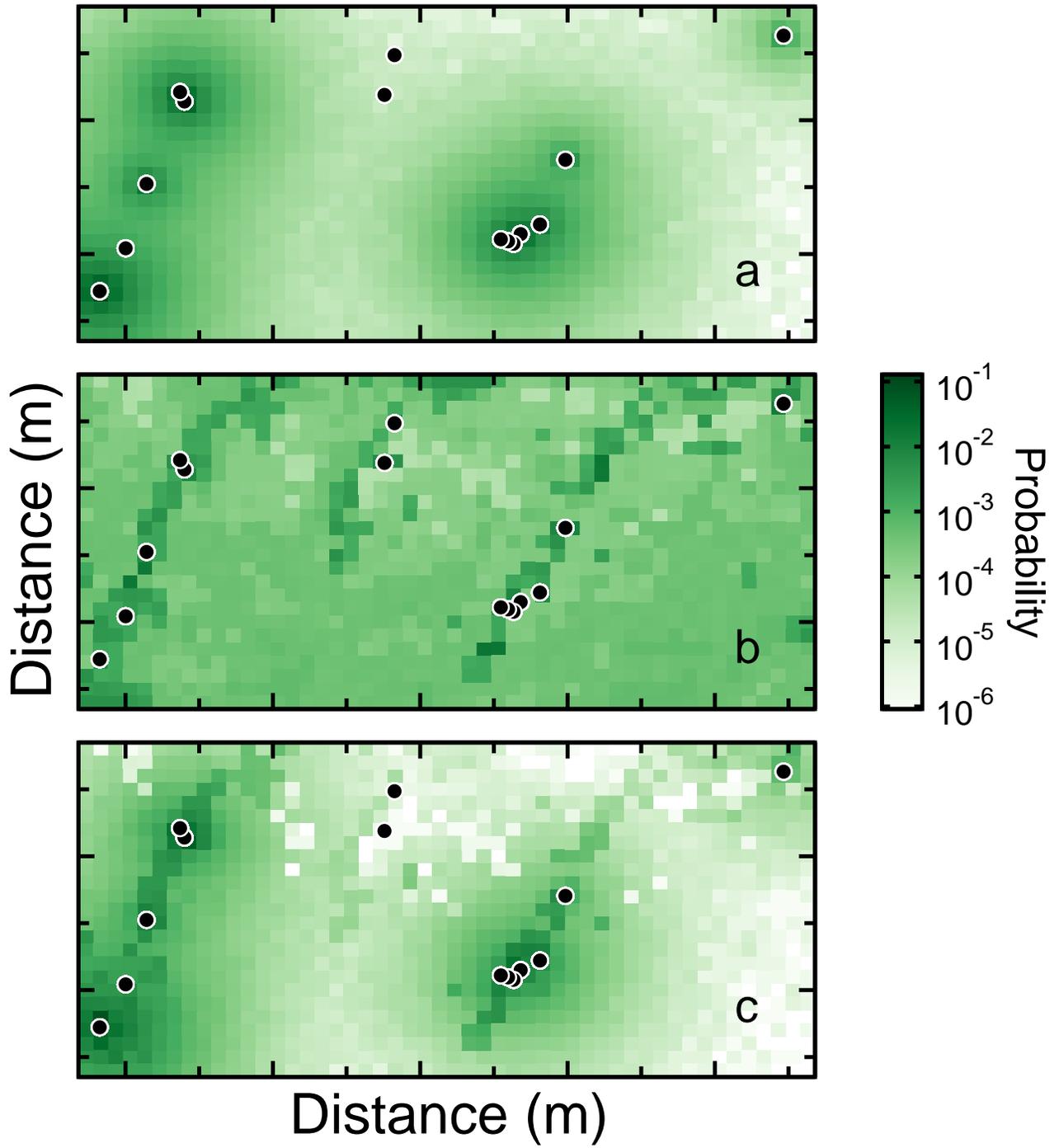


Figure 3

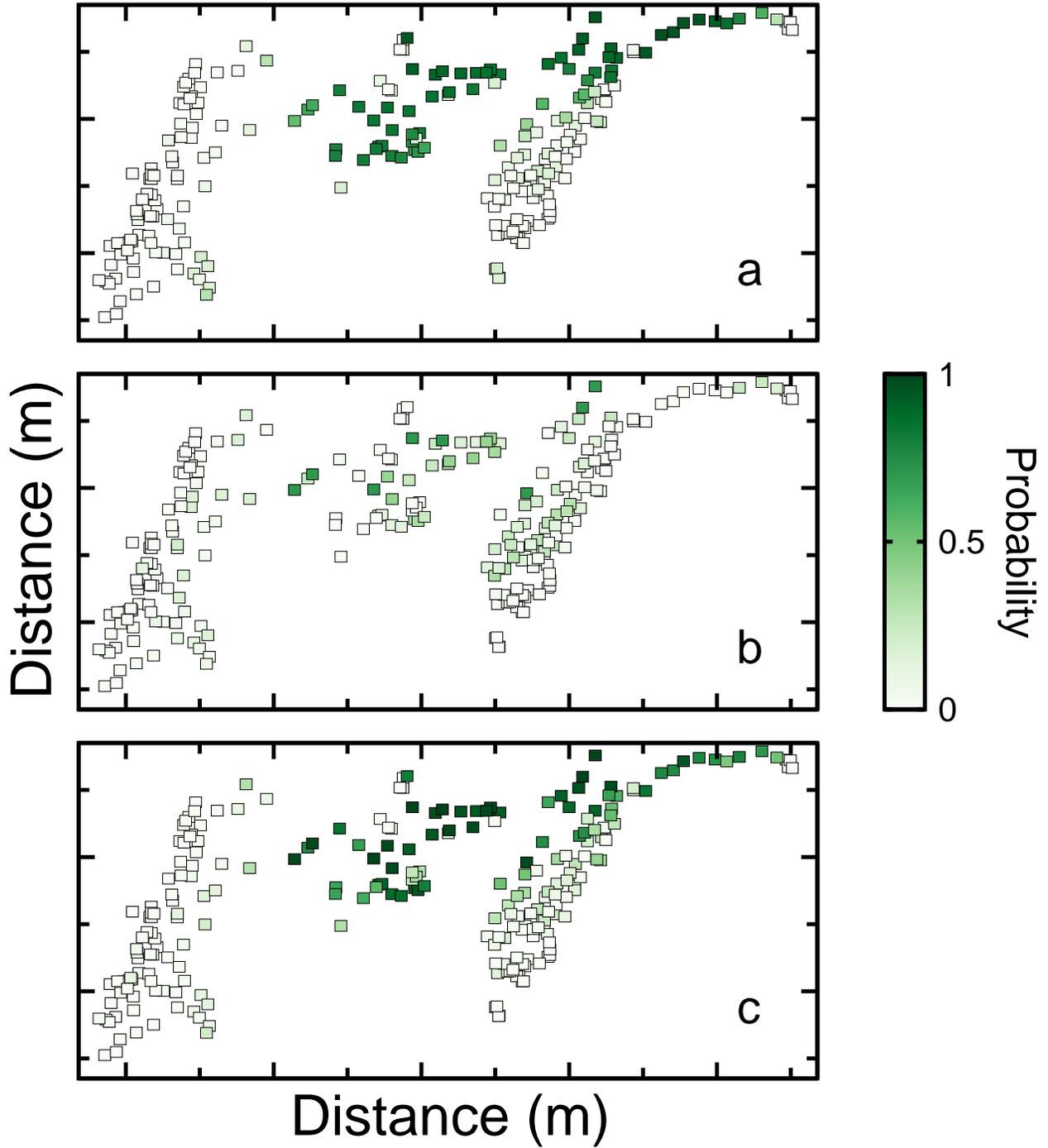


Figure 4

