Assisting seed dispersers to restore old-fields: an individual-based model of the interactions among badgers, foxes, and Iberian pear trees

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ABSTRACT

1. Increasing land abandonment in many areas of the world presents an opportunity for ecosystem recovery, which is often driven by seed dispersal by vertebrate frugivores. However we are far from understanding the most effective way of using common management actions (i.e. planting fruiting trees) to stimulate animal seed dispersal and thus the restoration of human-altered abandoned habitats.

2. To investigate how to stimulate animal seed dispersal, we combined long-term field data with individual-based, spatially explicit simulation models. We used our approach to assess the effectiveness of contrasting Iberian pear *Pyrus bourgaeana* planting strategies in enhancing restoration of abandoned lands through seed dispersal by red foxes *Vulpes vulpes* and Eurasian badgers *Meles meles* in the Doñana World Biosphere Reserve (South West Spain).

3. Our simulation results indicate that planting trees in an aggregated fashion is less efficient in terms of seed arrival than planting them regularly or randomly. For example, for aggregated planted trees the increase in the area of the oldfield that received seeds was only 7-9% compared to the baseline scenario of no intervention, whereas for regularly distributed planted trees the increment was up to 40%.

4. Doubling the number of planted *P. bourgaeana* trees appeared cost-effective for regular and random tree distributions, but not for the aggregated one. For example, while doubling the number of trees planted regularly lead up to 12% increase in the number of seeds arriving into the oldfield, no increment on the number of arrived seeds was detected when trees were planted aggregately.

5. *Synthesis and applications*. Choosing the spatial distribution and density of planted trees in abandoned lands depends on a number of ecological and socio-economical factors. Given our results, the strong seed dispersal limitation of the target tree population and the fact that our study site was fully protected for conservation, planting *Pyrus bourgaeana* trees regularly appeared to be the most efficient strategy to enhance seed arrival into the target oldfield. Combining long-term field data with individual-based, spatially explicit simulation models has a strong potential to guide local restoration efforts in diverse human-altered habitats and, thus, to bridge the existing gap between basic and applied research on animal seed dispersal.

Keywords: Abandoned lands, agent-based modelling, dispersal kernel, Doñana National Park, endozoochory, frugivory, oldfields, restoration, seed dispersal limitation, tree planting

INTRODUCTION

Environmental and socio-economic changes are causing increased levels of land abandonment worldwide, leading to noticeable changes in land cover (Cramer et al. 2008, Blondel et al. 2010, Queiroz et al. 2014). In the European backcountry, forests and scrublands are spreading due to the decline of agricultural practices, pastoralism, and forest activities (Thomson 2005). Land abandonment can represent an opportunity for ecosystem recovery into historical states previous to human disturbances (Lamb, Erskine & Parrota 2005). Restoring abandoned lands is therefore a common, though complex, goal which unquestionably benefits from science-based guidance (Standish et al. 2007, Rey-Benayas et al. 2008, Zahawi et al. 2013).

Seed dispersal by vertebrate frugivores is an important element for successful woody recolonization of both natural and human altered landscapes (Verdú and García Fayos 1998, Kremen et al. 2007, Escribano-Avila et al. 2014). In particular, the intensity and spatial pattern of seed arrival regulates the speed and outcome of endozoochorous colonization (i.e., dispersal of seeds via ingestion by animals) (Jordano and Schupp 2000, Fedriani and Wiegand 2014). In humanized landscapes, however, fragmented source plant populations and shortage of efficient vertebrate seed dispersers frequently leads to deficient 'propagule pressure' (*sensu* Lockwood et al. 2005). Arrival of seeds in low numbers makes establishment unlikely, particularly under the harsh abiotic conditions of arid and Mediterranean habitats (Maestre et al. 2005). Consequently, a common restoration practice to enhance seed arrival and to trigger nucleation processes (e.g. Verdú and García-Fayos 1998, Pausas et al. 2006) in abandoned lands consists in planting fruiting trees of suitable target species (e.g. Stanturf et al. 2014). In addition to enhance seed arrival, planted trees can also facilitate recruitment and establishment (Rey-Benayas et al. 2008). However, we are far from understanding the most effective way of planting fruiting trees to stimulate the natural restoration of human altered habitats.

It has been proposed that planting trees with aggregated patterns could be an economically feasible way of reconciling agricultural practices, ecological restoration, and conservation in agro-ecosystems (Rey-Benayas et al. 2008). The argument is that planted woodland islets may act as sources of woodland species and seeds, which may accelerate woodland development (Zahawi et al. 2013). However, while aggregated trees could be visited more frequently by some seed dispersers than isolated trees (Carlo and Morales 2008, Pegman et al. 2016), seed dispersal distances decrease as fruiting trees become more aggregated because frugivore activity concentrates in few fruit source areas (Pegman et al. 2016). While planting more trees is expected to speed up the recolonization of abandoned lands (also called 'oldfields'; *sensu* Cramer et al. 2008), it also increases cost and alters the cost-effective trade-off. Thus, the question arises what combination of density and spatial distribution of planted trees is most effective in oldfield restoration? More specifically, how could managers maximize the seed rain generated by vertebrate frugivores into oldfields by planting fruiting trees of target species?

Clearly, the optimal combination of density and spatial pattern of planted fruiting trees will depend critically on the biological characteristics of the oldfield, the nature of the species being dispersed, and the associated frugivores. For example, the patterns of frugivore movement, seed retention times in the guts, and their habitat use are essential aspects to accurately predict seed dispersal patterns (Levey et al. 2008, Côrtes and Uriarte 2013). Predicting seed dispersal kernels into oldfields represents a major research challenge for biodiversity restoration that demands integrative approaches that go beyond field studies. In the case of animal-dispersed plants, understanding and predicting seed rains require a multidisciplinary approach, including seed dispersal ecology, animal movement and behaviour, and ecological modelling (Levey et al. 2003, Russo et al. 2006, Côrtes and Uriarte 2013). Fortunately, recent techniques of individual-based and spatially explicit modelling (e.g. Wiegand et al. 2003, Grimm and Railsback 2005, Railsback and Grimm 2012, Ayllón et al. 2016) allow for an integration of such diverse sources of information into a simulation model. This provides means for investigating how the density and spatial distribution of planted trees, in conjunction with dispersers' behaviour and physiology, determines the pattern and intensity of seed rains into oldfields.

In this study, we illustrate the potential of combining long-term comprehensive field studies with individual-based, spatially explicit simulation models (hereafter IBSEM) to assess the effectiveness of contrasting tree planting strategies in enhancing restoration of abandoned lands. To this end, we developed a IBSEM (called '*DisPear*') combining data concerning: *i*) the spatial distribution, crop size, and fruit ripening behaviour of trees, *ii*) detailed movements and habitat use of seed dispersers, and *iii*) seed retention times in the guts and faecal delivering patterns of seed dispersers. To assess the effect of different tree planting strategies on seed dispersal into the oldfield, we varied the density and spatial distribution of planted trees (Rey-Benayas et al. 2008, Stanturf et al. 2014), as well as the response of seed dispersers to contrasting tree spatial distributions.

We applied our model to an oldfield located within the Doñana World Biosphere Reserve (SW Spain) where the Iberian pear *Pyrus bourgaeana* is a key representative of the endozoochore flora and is dispersed mainly by Eurasian badgers *Meles meles* and red foxes *Vulpes vulpes* (Fedriani et al. 2010, 2012). The Doñana area and the target oldfield have been subject to reiterative restoration efforts, with intensive planting of Iberian pears and other tree and shrub species (López-Pasarín 2004, García-Novo et al. 2007, Fedriani et al. 2017). However, these efforts have been largely unsuccessful (Fedriani et al. 2017). The results of our simulation experiments with *DisPear* provide valuable guide to maximize the effectiveness of restoration efforts by taking advantage of "passive restoration" by dispersers-generated seed rains in our and other oldfields.

MATERIALS AND METHODS

Study site

Our focal oldfield is located within the Doñana World Biosphere Reserve, SW Spain (elevation 0–80, Fig. 1). The climate is Mediterranean sub-humid, characterized by dry, hot, long summers (June–September) and mild, wet winters (November–February). Within our study site all Iberian pear trees are located in Mediterranean scrubland, which is dominated by the evergreen shrubs *Pistacea lentiscus, Chamaerops humilis, Halimium halimifolium, Cistus* spp., with some scattered *Quercus suber* and *Olea europaea* var. *sylvestris* trees. In the eastern portion (~310 ha) of the scrubland, all Iberian pear trees and most other trees and shrubs were mechanically removed during 1970, resulting in a continuum of grasslands with virtually no understory of Mediterranean scrubs (Fig. 1). The area was then used for intensive cow grazing until 1996, when the land was expropriated by the Spanish National Park Service and the cows removed (López-Pasarín 2004). Since then, the recolonization of this oldfield by historical woody species, specially by Iberian pear, is occurring at a very slow speed due to limited seed arrival and low seedling establishment related to extreme summer droughts and herbivory (Fedriani and Delibes 2009a, Fedriani et al. 2010, Authors *unpublished data*). A detailed description of the study area habitat composition is included in the model’s description provided in Appendix S1.

Study species

Pyrus bourgaeana Decne (Rosaceae) is a small (3–6 m height) deciduous tree endemic to the Iberian Peninsula (Spain, Portugal) and North Africa (Morocco). In the Doñana area, its distribution is very fragmented, with trees occurring at low densities (generally < 1 individual ha^{-1}). However, tree local distribution varies from highly isolated to strongly aggregated (6–8 reproductive individuals within ~25 m; Fedriani et al. 2010). The establishment and persistence of such Iberian pear clusters arise from dispersal limitation and spatial contagion of dispersed seeds (Fedriani et al. 2010, Fedriani and Wiegand 2014). The Doñana population of Iberian pear has limited reproduction and regeneration ability (Fedriani et al. 2010, 2012) and shows a marked left-skewed demographic structure, with many individuals in older age classes, few juveniles, and even fewer seedlings and saplings (Authors *unpublished data*). Recurrent local restoration efforts have attempted to mitigate this situation, though with limited success (e.g. López-Pasarín 2004, García-Novo et al. 2007).

Each tree usually produces yearly between 200-700 fruits. After ripening, they drop to the ground from September to December and are harvested by a diverse assemblage of frugivores (Fedriani and Delibes 2013). Local effective seed dispersers are mostly medium-sized mammalian carnivores (badger and red fox; Fedriani and Delibes 2013), which occur in low densities (Fedriani et al. 1999). Seedlings emerging from seeds dispersed by carnivores are often observed in both laboratory (up to 20%, Fedriani and Delibes 2009b) and field conditions (Fedriani and Delibes 2009a). In particular, different cohorts of *P. bourgaeana* seedling are regularly found in badger latrines and, less frequently, in fox faecal deposition sites (Fedriani and Wiegand 2014; Authors *unpublished data*). Despite its low population density, Iberian pear fruit, seeds, seedlings, and leaves represent important resources for diverse animal guilds, especially during the dry summers (Fedriani et al. 2012).

Habitat usage and movements of both foxes (n = 31) and badgers (n = 17) has been studied in detail at our study site by telemetry (e.g. 24-h periods, with dispersers being located at 1-h intervals; Fedriani et al. 1999, Revilla and Palomares 2002). In general, during daytime both foxes and badgers are inactive hidden in their den, while during sunset they (especially foxes) tend to move towards the oldfield where they remain active during most nighttime. Since both carnivores intensively feed on Iberian pear fruits during the autumn and early winter, they disperse some seeds into the oldfield (Fedriani and Wiegand 2014) where seedlings often emerge. However, because of extreme summer droughts and intensive seedling herbivory by rabbits and deer, Iberian pear recruitment and establishment in the oldfield seldom occur (Fedriani et al. 2012, Authors *unpublished data*).

Model description

A full and detailed model description following the ODD protocol (Grimm et al. 2010) is provided in the Appendix S1. The model was designed to simulate the seed rain of Iberian pear in oldfields which emerges from the interaction between the behaviour of its mammalian seed dispersers and the abundance and spatial distribution of fruiting trees (both wild and planted ones). Our specific objective is to assess the effectiveness of fruiting tree planting, a commonly used restoration action in oldfields. To this end we analyze how contrasting densities and distributions of planted fruiting trees affect the speed and spatial pattern of oldfield recolonization.

Our spatially-explicit individual-based model *DisPear* simulates seed production of fruiting trees, as well as movement, seed consumption and seed dispersal by endozoochorous seed dispersers in a spatially structured landscape (Fig. 1). The interaction between fruiting trees and animal behaviour generates a seed dispersal kernel (Bullock et al. 2017), our main target. *DisPear* was implemented in NetLogo 5.0.3 (Wilensky 1999) and is mechanistic, stochastic, and event driven. The model spatial extent (total area is ~1840 ha) is a rectangular landscape of 221 × 208 patches or cells and represents the area around the oldfield in the Doñana World Biosphere Reserve (Fig. 1; see also Appendix S1). The model reads the habitat type of each cell (20 × 20 m) that define the landscape as well as the location of trees from an input file.

Briefly, we model Iberian pear seed dispersal by red foxes and badgers under different restoration scenarios (i.e. density and distribution of planted trees) and analyze their influence on oldfield recolonization. The model has six kinds of entities (see Table S1 in Appendix S1): *i*) dispersers (foxes or badgers) that move across the landscape; *ii*) spatial-groups that represent the area where the social groups of dispersers centre their activities; *iii*) a grid of patches of 20 × 20 m^2 that define the landscape and where each patch can represent a different habitat type; *iv*) fruiting trees that constitute a specific habitat type; *v*) fruits that are produced by Iberian pear trees and become available to seed dispersers once they fall and ripe; and *vi*) disperser faeces that are delivered by dispersers and may contain seeds. A full description of state variables of entities appears in Table S1.

The model considers five main processes: one involving fruiting trees (fruit dropping), one involving fruits (status and age updating), and three performed by dispersers (movement, fruit uptake, and fruit delivery). Patches and faeces do not perform any active process. All processes take place at an hourly time step, except fruit dropping that occurs only at the beginning of the day (i.e. once every 24 time steps).

Disperser movement is based on extensive telemetry data on habitat use and the distance travelled during one hour, depending on the circadian cycle (Fig. S1; e.g. Fedriani et al. 1999). Dispersers sense and can feed on fruits within a corridor around their movement path, and might also defecate depending on the gut retention times of ingested fruits. Based on certain probabilities (Table S2 of Appendix S1), dispersers will eat fruits, if there is a fruiting tree in the corridor with available fallen fruits. Foxes will then defecate at a randomly chosen patch within their movement corridor whereas badgers defecate at a patch within the corridor previously used for defecation if existing. This rule resembles latrines used by badgers. The ecological rationale underlying the movement rules is detailed in Appendix S3.

Other elements in our model reflect the ecology of this tree-seed dispersers interaction and include: 1) fallen ripe fruits can become unavailable due to different causes (consumption by fruit predator, rotting, etc.), 2) seed dispersers sense their den location and they tend to come back to their den during sunrise and keep mostly inactive there during daytime, and 3) because red foxes and, especially, Eurasian badgers live in social (or spatial) groups composed of several individuals, the model represents spatial groups of foxes and spatial groups of badgers (for our study site we assume two groups of each species). Dispersers sense to which spatial group they belong to and thus direct their movements within their home range, although occasionally they can move out of their respective home range, a pattern that is consistent with field observations.

Model parameterization and validation

DisPear was developed, parameterized and tested following the pattern-oriented framework (Wiegand et al. 2003, Grimm et al. 2005, Grimm and Railsback 2005). Parameter values (41 parameters; Table S2) were estimated from four sources of information: field observational data, experimental data, calibration, and expert knowledge.

The value of 21 parameters were directly obtained from published field studies (Table S2), and four parameters concerning the seed retention times were estimated from unpublished results of an experimental feeding trial where three captive foxes and two captive badgers were offered Iberian pear fruits during three consecutive days (Authors *unpublished data*,

Table S2). To assist parameterization in cases where no data was available, or where we suspected a high sensitivity of model outputs to a parameter, we conducted a global sensitivity analysis (for a full description of sensitivity analysis see Appendix S2). The values of 15 parameters, for which data was not available, were guesstimated based on our expert knowledge of the study system gathered during more than two decades of field research. Finally, we calibrated the value of five parameters to which model outputs were highly sensitive and which were very uncertain (no data available). To do this, the biologically plausible range of each parameter was covered by five equidistant values and all potential combinations (3125 parameter sets) were simulated and replicated five times. The optimal parameter set was the one that was able to reproduce the highest number of patterns observed in the field. We then used an additional trial-and-error adjustment for the parameters defining the time elapsed for dispersers between consecutive fruits eating bouts (time-between-eating-fox, time-between-eating-badger) because they are the main drivers of faeces abundance and clustering (Appendix S2).

To assess the performance of *DisPear*, we used its final parameterization (Table S2) to conduct 100 replicates of simulations and compare the simulated outputs to 46 observed field patterns describing *i*) dispersers' movement (10 patterns), *ii*) dispersers' habitat use (30 patterns), and *iii*) fruits and faeces abundance and spatial distribution and clustering (6 patterns). We calculated the deviation Δ (%) of the simulated output (SO) from the observed pattern (OP) as: D =100* (SO – OP)/OP.

Simulation experiments

We conducted a series of simulation experiments to assess whether and how Iberian pear seed arrival into the oldfield is influenced by (i) the density and distribution of planted trees and

(ii) by the preference of seed dispersers for aggregated versus isolated fruiting trees. We used two typical tree densities or planting efforts (15 or 30 planted trees) and three tree distributions (aggregated, random, regular; Fig. 2) to account for potential logistical and budgetary constraints of different restoration campaign designs (Rey-Benayas et al. 2008, Stanturf et al. 2014). The three simulated trees distributions (Fig. 2) were generated as follows: (*i*) by randomly generating their coordinates within the oldfield (i.e. random distribution), (*ii*) by distributing the simulated trees within a grid (regular distribution) of seven columns and up to six rows. Distance between consecutive columns was 360m; distance between consecutive rows within a column 300m, and (*iii*) by distributing all trees within three cells (either five or ten trees per cell) separated by 360m (aggregated distribution).

Several studies indicated that frugivores tend to visit more often aggregated fruiting trees (e.g. Carlo and Morales 2008). However, in Doñana foxes and badgers tend to forage underneath isolated rather than aggregated Iberian pear trees, possibly to avoid competition with ungulate fruit predators which concentrate in tree aggregations (Authors *unpublished data*). Therefore, we evaluated three typical scenarios regarding the disperser preference for aggregated and isolated trees: (*i*) dispersers visit aggregated and isolated trees with the same probability, (*ii*) the probability to visit isolated trees doubled that of aggregated ones, (*iii*) the probability to visit aggregated trees doubled that of isolated ones. By using a full factorial design (2 tree densities × 3 tree spatial distributions × 3 dispersers preferences), we aimed to identify the combination of factor levels leading to the most effective restoration strategy under different scenarios of disperser preferences (i.e. the one that maximises Iberian pear seed arrival into the oldfield). Restoration scenarios were compared to a baseline scenario without planted trees, in which dispersers visit with the same probability aggregated and isolated trees.

For each combination of factors, we ran 100 simulations, with each replicate comprising 1800 time steps or hours (i.e. 75 days × 24h). The time period modeled (75 days) represents the 'dispersal season' from mid September to the end of November, when ripe *P. bourgaenea* fruits are available to dispersers (Fedriani et al. 2012).

We analysed the effects of the different restoration strategies on five model outputs or response variables: number of fox- dispersed seeds arriving to the oldfield, number of badger-dispersed seeds arriving to the oldfield, number of oldfield cells receiving seeds from aggregated trees, number of oldfield cells receiving seeds from isolated trees, and total number of oldfield cells receiving seeds.

Initial conditions

The landscape was composed of 221 × 208 patches 20 × 20m in size (Fig. 1). This spatial resolution was chosen to account for the observed small scale aggregation of *P. bourgaeana* trees (Fedriani et al. 2010). Most of the disperser activity occurs within the scrubland and the oldfield, the distinctly preferred habitats by both foxes and badgers. The model space is therefore represented as bounded. We used the observed locations of *P. bourgaeana* (*n* = 266) in the scrubland and those planted in the oldfield as seed sources (Fig. 2).

We assigned each disperser (five foxes and five badgers; Fedriani et al. 1999) randomly an initial home patch (called den) that was typically located within the scrubland near its border with the oldfield (80% and 90% of times, for badgers and foxes, respectively). In the remaining 20 and 10% of the cases, the initial home patch of each disperser (the den) is assigned randomly in open habitats (e.g. oldfield, marshes; Fedriani et al. 1999).

Data analysis

To estimate the relative importance of the three main factors (number of planted trees, distribution of planted trees, dispersers preferences of aggregated *vs*. isolated trees), we partitioned the total variation of each of the five response variables (see above "*Simulation experiments*") by analyzing the variance components. To this end, we used the Mixed procedure of SAS (SAS Institute 2016) and, as required for variance partitioning, the three factors were considered as random effects. 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 any statistical test to contrast model outputs across the different scenarios (White et al. 2014).

RESULTS

Model parameterization and output verification

Results of the simulations with the final parameterization indicate that the model was able to reproduce the range of values of the numerous empirical patterns relatively well (see Fig. S2 in Appendix S4). Specifically, most patterns concerning disperser habitat usage (70-86.7%; *n* = 30) were simulated with deviations from the observed patterns below 40-50%. As for the hourly distances travelled by dispersers, the fit was better, with the 80% and 90% (n = 10) of the patterns being reproduced with deviations from the observed patterns below 20% and 25%, respectively (Fig. S2). Finally, though the model showed a somewhat lower match to the faecal delivery patterns, most patterns (66.7%, n = 6) were simulated with deviations below 40% (Fig. S2).

Effect of restoration effort and strategy on the fox-generated seed rain

The three tested factors (density, configuration, disperser preference) explained between 29.2-57.1% of the total variance of most response variables (Fig. 3) which, following Møller and Jennions (2002), can be considered as well-predicted. The simulated number of fox-dispersed seeds reaching the oldfield per season ranged from 35 to 183 (mean ± 1SE, 80.4 ± 0.45). Most of the explained variance in the number of red fox-dispersed seeds arriving to the oldfield (83.1%) related to the distribution of planted trees (Fig. 3), whereas the number of planted trees explained a 16.9%. Tree planting augmented the number (Fig. 4A) and spatial extent (Fig. 2) of fox-dispersed seeds arriving to the oldfield as compared to the baseline scenario. Planting trees with random or regular patterns substantially increased the number and spatial extent of fox dispersed seeds whereas planting trees in an aggregated way was the least effective strategy (i.e. only 6.6% increment compared to the baseline). Aggregating planted fruiting trees within a few patches likely reduced the probability that foxes found them. Doubling the number of planted trees (from 15 to 30) had a small effect on the number of fox-dispersed seeds reaching the oldfield when they were aggregated but rendered a major enhancement for randomly and regularly planted trees (16.8% and 12.3%, respectively; Fig. 4A).

Effect of restoration effort and strategy on the badger-generated seed rain

In contrast to the trend for fox seed dispersal, variations in the three tested factors only explained 4% of the variance in the number of badger-dispersed seeds arriving to the oldfield, and thus such results must be taken with caution. The simulated number of badger-dispersed Iberian pear seeds reaching the oldfield per season varied from 13 to 219 (80.4±0.45). As for the fox-dispersed seeds, most of the explained variance in the number of badger-dispersed seeds reaching the oldfield was related to the distribution of planted trees (97.5%; Fig. 3), whereas the number of planted trees only explained 2.5% of the variance. Planting trees randomly and regularly markedly increased the spatial extent (Fig. 2) and number of badger-dispersed seeds reaching the oldfield (38.8% and 34.8% compared to the baseline, respectively; Fig. 4B), whereas planting aggregated trees had only a small effect (9.1% increase; Fig. 4B). Interestingly, doubling the number of planted trees leads only to small increases in the number of badger-dispersed seeds reaching the oldfield for all three tree distributions (1.2%, 3.3% and 5.6% for aggregated, random, and regular distributions, respectively; Fig. 4B). For completeness, Figure 4C shows the effect of tree planting on the total number of oldfield cells receiving dispersed seeds.

The effect of planting tree on overall the dispersal kernels

Planting trees into the oldfield clearly enlarged the dispersal kernels regarding the baseline scenario of no planting trees for random and regular distributions (Fig. 2); however, such effect was much weaker when trees were planted in a aggregated fashion (Fig. 2). We also evaluated whether a less tight tree clustering (i.e. six clusters with five trees per cluster) would change our conclusions. Results from these new simulations (not shown) confirmed that the aggregated distribution lead always to much less intensive seed rains than the regular and random tree distributions. Finally, we quantified variation in the number of oldfield cells (patches) receiving seeds from both aggregated and isolated trees (i.e. those with and without neighbours within 20m, respectively; Fig. 5). As expected, the number oldfield cells receiving seeds from aggregated trees increased when planted trees were aggregated (55.7±0.55) as compared with either random (46.68±0.45) or regularly (47.44±0.47) tree distributions (Fig. 5). Also, the number oldfield cells receiving seeds from aggregated trees also increased as the preference of dispersers for aggregated trees increased (Fig. 5).

DISCUSSION

Intriguingly, despite commendable research efforts and the fact that plant species that are planted during costly restoration programs are often the same that are naturally dispersed by animals (Jonson 2010), basic research on seed dispersal and restoration are not well integrated yet. Here, we used long-term field data on the ecology and movements of two seed dispersers, the reproductive biology of a tree species colonizing an oldfield, and the ecology of a plant-disperser interaction to model the seed dispersal kernels (Bullock et al. 2017) into an oldfield. Our multidisciplinary approach makes specific predictions concerning the effectiveness of contrasting strategies of planting trees that can guide ongoing local restoration efforts (ADAPTAMED 2015, Fedriani et al. 2017), helping to bridge the existing gap between basic research on seed dispersal and applied investigations on ecological restoration.

Sensitivity analysis

The model and its final parameterization based on extensive telemetry (e.g. Fedriani et al. 1999) and field observational and experimental data (e.g. Fedriani et al. 2010) is a powerful tool to simulate the seed rain arriving at our modelled oldfield under different scenarios. Given the large amount of empirical patterns involved in model and the good fit between model outputs and the corresponding values observed in the field for most patterns tested (n =

46), our model provides reasonably accurate predictions for the ecological questions addressed.

Our global sensitivity analysis (Appendix S2) showed that the model parameters related to dispersers' spatial behaviour have the strongest influence on most model outputs. In particular, the mean distances travelled during the different periods of the circadian cycle strongly drive habitat use and seed dispersal patterns (Fig. 2), and thus the intensity of the seed rain into the oldfield (Fedriani et al. 1999, 2010). Fortunately, the parameterization of the distances travelled are very reliable as they were derived from detailed telemetry studies.

Management implications: what is the best tree planting distribution to enhance seed dispersal into oldfields?

Our simulation results have important consequences for restoration of abandoned lands. Planting trees in an aggregated fashion was less efficient in terms of seed arrival that planting them in a regular fashion (but see Zahawi et al. 2013). For aggregated fruiting trees we observed in our simulations the lowest number of seeds dispersed by foxes and badgers as well as the lowest fraction of oldfield receiving seeds (Fig. 2). Also, we found the unexpected result that doubling the number of trees planted in an aggregated way (from 15 to 30 trees) did not enhance seed arrival into the oldfield. This finding, that comprises an important message for managers, seemed related to three non-exclusive mechanisms: (*i*) dispersers in the model may often miss the few existing tree aggregations within the oldfield especially if they are located far from the border of the oldfield, (*ii*) dispersers may becoming quickly satiated once they find a tree aggregate (usually ingesting up to two fruits per feeding bout; Fedriani and Delibes 2013) and cannot benefit from the additional trees planted in the aggregates, and (*iii*) they may spend more time in tree aggregates and disperse most seeds underneath planted trees (e.g. Uriarte et al. 2011, Pegman et al. 2016). Furthermore, because short-distance seed dispersal dominates when trees are aggregated (Fedriani et al. 2010), tree expansion and coalesce over time of tree aggregations seems unlikely. Therefore, under some circumstances (see below), managers should avoid planting trees in an aggregated fashion.

We focused on the seed arrival into the oldfield and, though seed arrival is a critical necessary condition for eventual seedling establishment and recruitment, it is not a sufficient condition (Schupp et al. 2010, Fedriani et al. 2012). Seedling establishment, growth, and survival could be more liming for eventual establishment than seed arrival. Tree aggregates could provide a more adequate microclimate than isolated trees promoting thus more recruitment and thereby balancing the lower seed arrival. However, tree aggregates increase intraspecific competition (Fedriani et al. 2015) as well as seedling herbivory by deer and rabbits (Authors *unpublished data*). On the other hand, our unpublished data indicates that the shade provided by a single Iberian pear could be enough to create a microhabitat with lower summer temperatures and higher humidity to enable seedling survival and recruitment (Authors *unpublished data*; e.g. Galindo-González et al. 2000, Herrera and García 2009). When planting *P. bourgaeana* juveniles, however, we recommend protecting them under local pioneer nurse species, such as the Mediterranean dwarf palm *C. humilis*, that lessen herbivory and also ameliorate water stress (Fedriani and Delibes 2011, Authors *personal observation*).

In these systems, several ecological factors should be taken into account when designing restoration actions. For instance, under shortage of seed dispersers, plants often experience seed dispersal limitation (e.g. Standish et al. 2007, Fedriani and Delibes 2011) often leading to adult aggregated distributions. This is the case of the Iberian pear in Doñana (Fedriani et al. 2010, 2012) where, in addition to marked dispersal limitation partly due to defaunation (Fedriani and Delibes 2011), this tree population experiences high level of seedling herbivory

(Authors *unpublished data*) and mortality induced by extreme droughts (Fedriani et al. 2012). In this and other similar ecological situations planting schemes should tend to counteract the strong aggregation caused by dispersal limitation and thus trees should be planted in regular distributions. However, in other areas of its distribution, Iberian pears show much higher population densities at lower level of spatial aggregation (Paton et al. 2002), suggesting thus relative adequate dispersal service and seedling recruitment. Under such situations, planted tree islets (Rey-Benayas et al. 2008) are likely to expand and coalesce over time and thus to accelerate natural recovery of abandoned lands with limited efforts and economical investment (Zahawi et al. 2013).

Managers' choice of the spatial distribution of planted trees should depend on a number of ecological and socio-economical factors (Rey-Benayas et al. 2008, Cole et al. 2010). For example, planting trees regularly is more expensive than planting aggregated trees (Rey-Benayas et al. 2008) and thus managers should incorporate this aspect into cost-effective trade-off considerations. In agricultural landscapes, owing to the variety of uses to which the non-planted land can be devoted, managers have to conciliate economic production and conservation of biodiversity and thus the use of woodland islets seems more suitable (Rey-Benayas et al. 2008). In other areas such as protected lands for conservation (e.g. National Parks) managers do not need to conciliate conservation and exploitation, the whole area could be potentially devoted to restoration and, thus, planting trees regularly should be the most appropriate approach.

To conclude, we suggest that in our study area and under a limitation of the number of trees to be planted, planting isolated Iberian pears would be more efficient than planting them in an aggregated fashion in terms of arrival of badger- and fox-dispersed seeds. The field of ecological restoration is a paradigm of the necessity and merits of interdisciplinary approaches to real-world problems (Gold *et al*. 2006). Our combination of long-term field research and ecological modelling provides managers with useful specific predictions concerning the effectiveness of contrasting planting trees schemes, and thus helps to bridge the existing gap between basic research on vertebrate seed dispersal and applied investigations on ecological restoration.

AUTHOR'S CONTRIBUTIONS

JMF, TW, DA, VG conceived and developed the model. JMF, DA analyzed the data. JMF, FP, AS gathered essential field data. JMF wrote the first draft. All authors significantly contributed to the final manuscript.

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DATA ACCESSIBILITY

DisPear model code and parameter values are available from figshare: https://doi.org/10.6084/m9.figshare.5280862.v1 (Fedriani et al. 2017).

REFERENCES

ADAPTAMED (2015). Protection of key ecosystem services by adaptive management of climate change endangered Mediterranean socioecosystems (LIFE 14 CCA/ES/000612).

Ayllón, D., Railsback, S.F., Vincenzi, S., Groeneveld, J., Almodóvar, A., & Grimm, V. (2016). InSTREAM-Gen: Modelling eco-evolutionary dynamics of trout populations under anthropogenic environmental change. Ecological Modelling, 326, 36-53.

Blondel J, Aronson J, Boudiou JY, and Boeuf G. 2010. The Mediterranean Basin – biological diversity in space and time. Oxford, UK: Oxford University Press.

Bullock, J.M., Mallada González, L., Tamme, R., Götzenberger, L., White, et al. 2017. A synthesis of empirical plant dispersal kernels. Journal of Ecology, 105, 6-19.

Carlo, T.A. and Morales, J.M. 2008. Inequalities in fruit-removal and seed dispersal: consequnces of bird behaviour, neighbourhood density and landscape aggregation. J. Ecol. 96: 609–618.

Cole, R.J., Holl, K.D., & Zahawi, R.A. (2010). Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. Ecological Applications, 20: 1255-1269.

Côrtes, M.C., & Uriarte, M. (2013). Integrating frugivory and animal movement: a review of the evidence and implications for scaling seed dispersal. Biological Reviews, 88(2), 255-272.

Cramer, V.A., RJ. Hobbs and R.J. Standish. 2008. What's new about old fields? Land abandonment and ecosystem assembly. Trends Ecol. Evol. 13: 104-112.

Escribano-Avila, G., Calviño-Cancela, M., Pías, B., Virgos, E., Valladares, F., & Escudero, A. (2014). Diverse guilds provide complementary dispersal services in a woodland expansion process after land abandonment. Journal of Applied Ecology 51: 1701-1711.

Fedriani JM and M. Delibes. 2009a. Functional diversity in fruit-frugivore interactions: a field experiment with Mediterranean mammals. Ecography 32: 983-992.

Fedriani JM and M. Delibes. 2009b. Seed dispersal in the Iberian pear *Pyrus bourgaeana*: a role for infrequent mutualists. Ecoscience 16: 311-321.

Fedriani JM and M. Delibes. 2011. Dangerous liaisons disperser the Mediterranean dwarf palm: defensive flesh-pulp role against seed predators. Ecology 92: 304-312.

Fedriani JM and M Delibes. 2013. Pulp feeders alter plant interactions with subsequent animal associates. Journal of Ecology 101: 1581-1588.

Fedriani JM and T. Wiegand. 2014. Hierarchical mechanisms of spatially contagious seed dispersal in complex seed-disperser networks. Ecology 95:514–526.

Fedriani, J.M., F. Palomares, and M. Delibes. 1999. Niche relations among three sympatric mediterranean carnivores. Oecologia 121: 138-148.

Fedriani, J.M., T. Wiegand, and M. Delibes. 2010. Spatial patterns of adult trees and the mammal-generated seed rain in the Iberian pear. Ecography 33: 545-555.

Fedriani JM, Zywiec M and M Delibes. 2012. Thieves or mutualists? Pulp feeders enhance local endozoochore recruitment. Ecology. 93:575–587.

Fedriani JM, T Wiegand, G Calvo, A Suárez-Esteban, M Jácome, M Żywiec, et al. 2015. Unraveling density and distance dependence of plant reproduction using a spatially explicit framework. Journal of Ecology 5: 1344–1353.

Fedriani JM, García L, Sanchéz M, Calderon J, and C Ramo. 2017. Long-term impact of protected colonial birds on a jeopardized cork oak population: conservation bias leads to restoration failure. Journal of Applied Ecology 54: 450–458.

Fedriani, J.M., Wiegand T., Ayllón D., Palomares F., Suárez-Esteban A., & V. Grimm (2017): *DisPear* model code implemented in NetLogo. https://doi.org/10.6084/m9.figshare.5280862.v1

Galindo-González, J., Guevara, S., & Sosa, V.J. (2000). Bat-and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. Conservation Biology 14: 1693-1703.

García-Novo, F., García, J.C.E., Carotenuto, L., Sevilla, D.G., & Faso, R.P (2007). The restoration of El Partido stream watershed (Doñana Natural Park): a multiscale, interdisciplinary approach. Ecological Engineering 30: 122-130.

Gold W, Ewing K, Banks J, et al. 2006. Collaborative ecological restoration. Science 312: 1880–81.

Grimm V, Revilla E, Berger U, Jeltsch F, Mooij WM, Railsback SF, et al. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310:987-991.

Grimm V, Railsback SF. 2005. Individual-based Modeling and Ecology. Princeton University Press, Princeton N.J., 428 pp.

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. Ecol. Model. 221, 2760–2768.

Herrera, J.M., & García, D. (2009). The role of remnant trees in seed dispersal through the matrix: being alone is not always so sad. Biological Conservation 142: 49-158.

Jonson, J. (2010). Ecological restoration of cleared agricultural land in Gondwana Link: lifting the bar at ‘Peniup’. Ecological Management & Restoration 11: 16-26.

Jordano, P., & Schupp, E. W. (2000). Seed disperser effectiveness: the quantity component and patterns of seed rain for Prunus mahaleb. Ecological Monographs 70: 591-615.

Kremen, C., Williams, N.M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., et al. (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecology letters 10: 299-314

Queiroz, C., Beilin, R., Folke, C., & Lindborg, R. (2014). Farmland abandonment: threat or opportunity for biodiversity conservation? A global review. Frontiers in Ecology and the Environment, 12(5), 288-296.

Lamb, D., Erskine, P.D., & Parrotta, J.A. (2005). Restoration of degraded tropical forest landscapes. Science 310: 1628-1632.

Levey, D.J., Tewksbury, J.J., & Bolker, B.M. (2008). Modelling long-distance seed dispersal in heterogeneous landscapes. Journal of Ecology 96: 599-608.

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20: 223-228.

López-Pasarín J. 2004. Restauración Ecológica del Coto del Rey (Dehesa Del Raposo, Caño Mayor y Matasgordas), Parque Nacional de Doñana. Organismo Autónomo Parques Nacionales. Technical report. 96 pp.

Maestre F.T., Valladares F. and J.F. Reynolds. 2005. Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. J. Ecol. 93: 748-757.

Møller, A., & Jennions, M.D. (2002). How much variance can be explained by ecologists and evolutionary biologists? Oecologia 132: 492-500.

Paton, D., Nuñez, J., Bao, D., & Muñoz, A. (2002). Forage biomass of 22 shrub species from Monfragüe Natural Park (SW Spain) assessed by log–log regression models. Journal of Arid Environments 52: 223-231.

Pausas, J. G., Bonet, A., Maestre, F.T., & Climent, A. (2006). The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. Acta Oecologica 29: 346-352.

Pegman, A.P.M., Perry, G.L., & Clout, M.N. (2016). Exploring the interaction of avian frugivory and plant spatial heterogeneity and its effect on seed dispersal kernels using a simulation model. Ecography.

Railsback, S.F., & Grimm, V. (2011). Agent-based and individual-based modeling: a practical introduction. Princeton university press.

Revilla, E., & Palomares, F. (2002). Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, *Meles meles*. Journal of Animal Ecology 71: 497-512.

Rey-Benayas, J.M., Bullock, J.M., & Newton, A.C. (2008). Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Frontiers in Ecology and the Environment 6: 329-336.

Russo S.E., S. Portnoy and CK Augspurger 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. Ecology: 87: 3160–3174.

SAS Institute. (2016). Base SAS 9.4 Procedures Guide. SAS Institute.

Schupp, E. W., Jordano, P., & Gómez, J.M. (2010). Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188: 333-353.

Standish, R.J., Cramer, V.A., Wild, S.L., & Hobbs, R.J. (2007). Seed dispersal and recruitment limitation are barriers to native recolonization of old-fields in western Australia. Journal of Applied Ecology, 44(2), 435-445.

Stanturf, J.A., Palik, B.J., & Dumroese, R.K. (2014). Contemporary forest restoration: a review emphasizing function. Forest Ecology and Management, 331, 292-323.

Thompson, J. D. (2005). Plant evolution in the Mediterranean. Oxford University Press on Demand.

Uriarte, M., Anciães, M., Da Silva, M.T., Rubim, P., Johnson, E., & Bruna, E.M. (2011). Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. Ecology 92: 924-937.

Verdú M., P. García-Fayos. 1998. Old-field colonization by *Daphne gnidium*: seedling distribution and spatial dependence at different scales. Journal of Vegetation Science 9: 713–718.

White, J. W., Rassweiler, A., Samhouri, J.F., Stier, A.C., & White, C. (2014). Ecologists should not use statistical significance tests to interpret simulation model results. Oikos 123: 385-388.

Wiegand, T., F. Jeltsch, I. Hanski, and V. Grimm. 2003. Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. Oikos 100: 209-222.

Wilensky, U., 1999. NETLOGO, Centre for Connected Learning and Computer-BasedModelling. Northwestern University, Evanston, IL, http://ccl.northwestern.edu/netlogo

Zahawi, R.A., Holl, K.D., Cole, R.J., & Reid, J.L. (2013). Testing applied nucleation as a strategy to facilitate tropical forest recovery. Journal of Applied Ecology 50: 88-96.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1: ODD-description of *DisPear* model.

Appendix S2: Sensitivity analysis.

Appendix S3: Reasoning of disperser's spatial behaviour.

Appendix S4. Level to which *DisPear* reproduced observed patterns.

Figure 1: Study site showing the location of the Doñana National Park in Southwestern Spain and the location of the studied oldfield within our study site in the northern portion of the National Park. The black disks in the scrubland represent the observed *P. bourgaenea* trees.

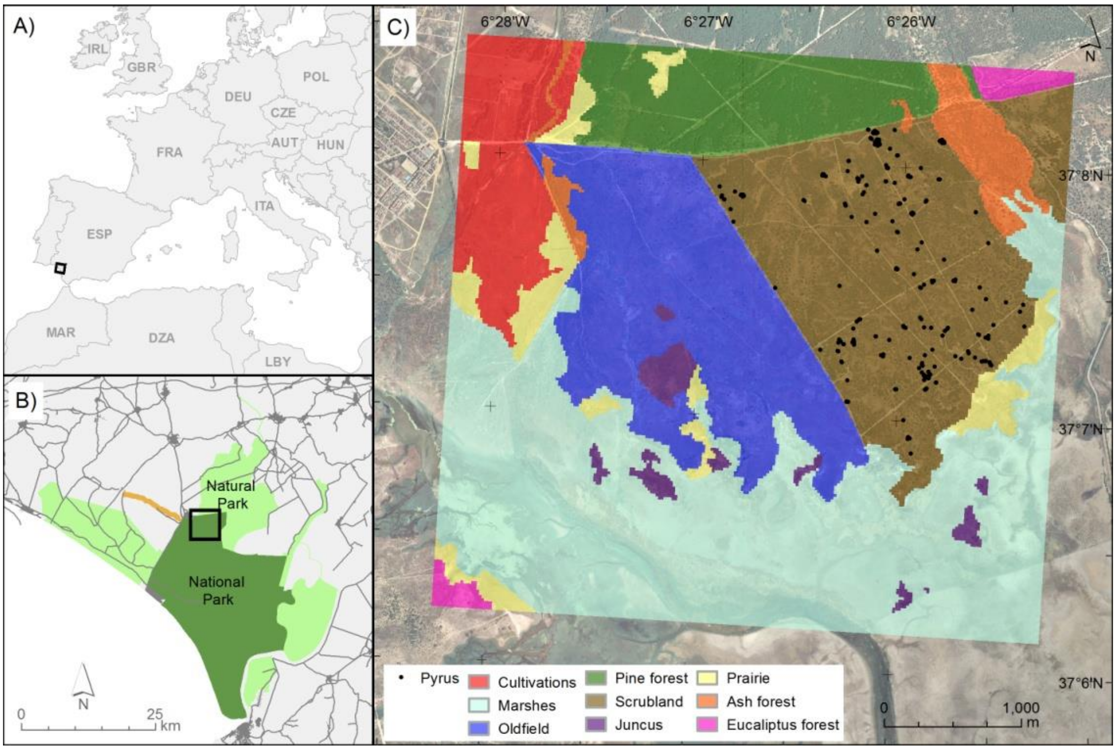

Figure 2: The different scenarios of planting trees in the old field (black dots) and its associated seed density kernels (accumulated during 25 years) for the baseline scenario (A), aggregately (B), randomly (C), and regularly planted trees (n = 30) (D). The black disks in the scrubland represent the observed *P. bourgaenea* trees. The color gradient of the dispersal kernels at the oldfield indicates the density of dispersed seeds, ranging from low (pale blue) to high density (red).

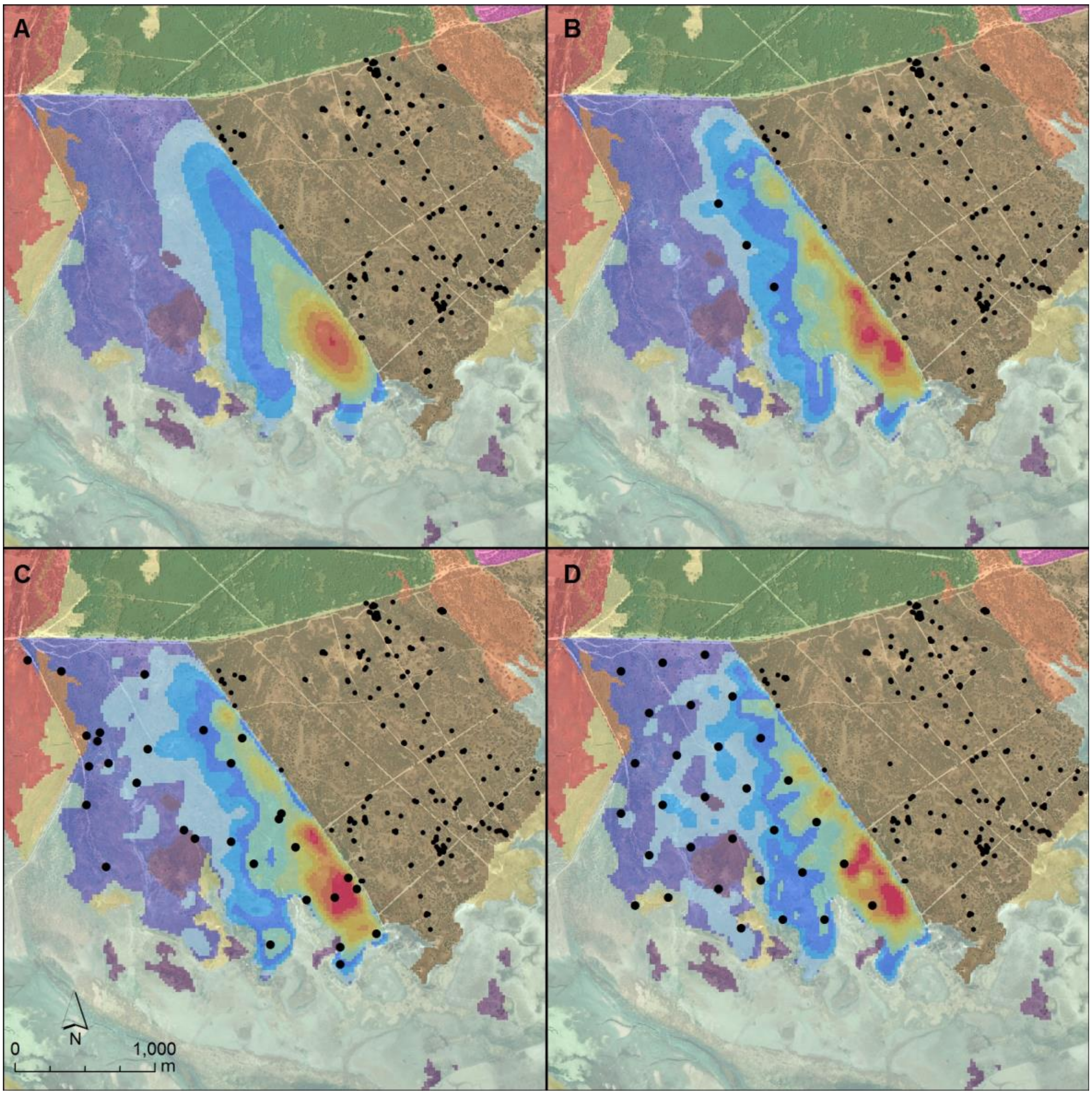

Figure 3: Percentage of variance of several model outputs explained by the three factors (number of planted trees, planted tree distribution, disperser preference). The model outputs included the number of oldfield cells receiving seeds, the number of oldfield cells receiving seeds from aggregated trees, the number of oldfield cells receiving seeds from isolated trees, and number of fox- and badger-dispersed seeds into the oldfield.

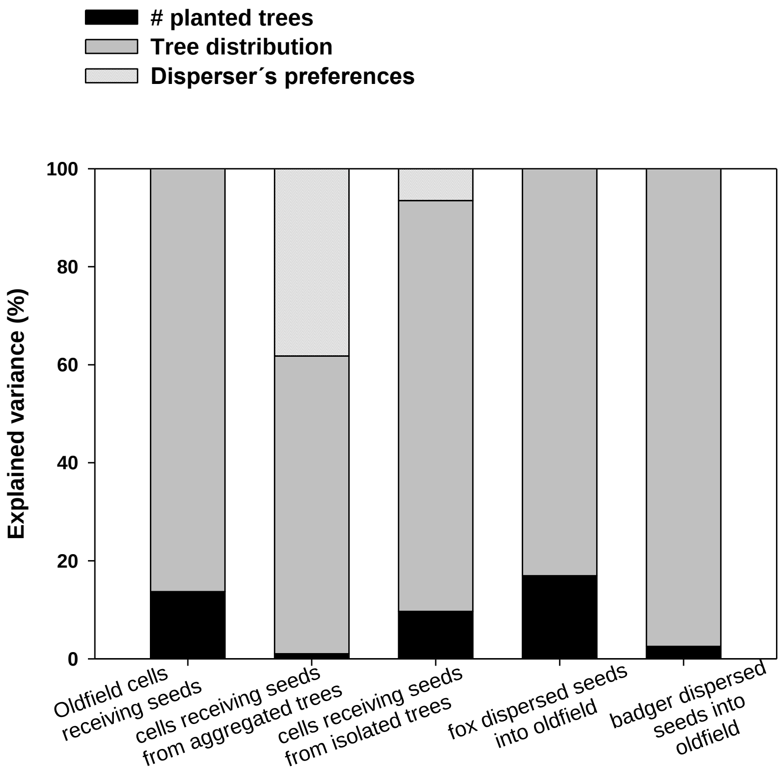

Figure 4: Effect of planted tree density and spatial distribution on a) the number of fox-dispersed seeds arriving into the oldfield, b) the number of badger-dispersed seeds arriving into the oldfield, and c) the number of oldfield cells receiving seeds. Bars represent mean ±95% confidence interval.

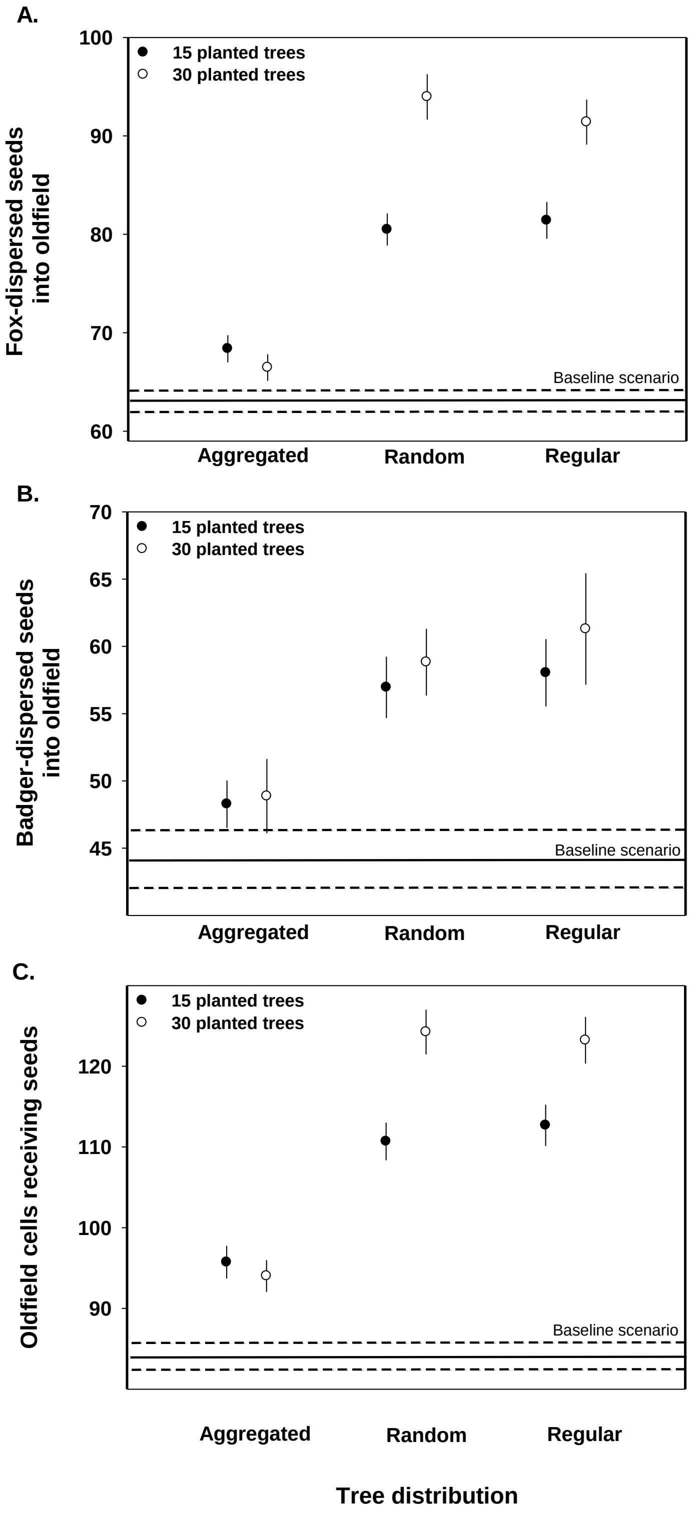

Figure 5: Combined effect of planted tree density, planted tree spatial distribution, and disperser preference of isolated *vs*. aggregated planted trees on the number of oldfield cells receiving seeds from aggregated and isolated trees.