Predicting forest management effects on oak–rodent mutualisms

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Wood mice *Apodemus sylvaticus* are the main dispersers of acorns in highly managed Mediterranean holm-oak woodlands. Mice mobilize and cache acorns to store them for winter consumption. They carry acorns away from potential competitors, face predation risks during mobilization, and cache acorns in areas where pilfering risks are low. However, mice can act either as net predators or as moderately efficient dispersers, depending on the way landscape management affects intraspecific competition for acorns and shelter availability. To assess the influence of landscape structure and mouse behavior on acorn dispersal, we developed an agent-based model (ABM) that translates forest management into changes in key environmental factors driving mouse foraging decisions.

The model was able to predict accurately acorn dispersal patterns in a wide range of forest management practices based on information on forest habitat availability, stem density and shrub cover. Sensitivity analysis revealed that caching rates emerged from the interplay between intraspecific competition for seeds and predation risk accepted during mobilization. It also showed that intraspecific competition for acorns decreased with increasing habitat loss (due to positive edge effects on acorn production) while landscape resistance to mouse movements increased. As a result, the net benefits of caching declined and acorn predation became the dominant strategy. Finally, we assessed the effects of shrub encroachment as a management practice to enhance dispersal services in savanna-like landscapes (dehesas). The model predicted non-linear responses with a 65% threshold of shrub cover needed to achieve relatively high levels of acorn dispersal. This value may not be compatible with the traditional exploitation of dehesas (livestock rearing). Our study shows that integrated approaches that combine environmental change driven by management with behavioral responses of dispersers improve our understanding of the causes of recruitment bottlenecks, and are useful tools for evaluating conservation strategies aimed at enhancing dispersal services.

Seed dispersal is a key component of plant population dynamics since it determines the potential area for recruitment and establishes the initial template for important post-dispersal process such as predation, competition and the spatial structure of mating networks (Nathan and Muller-Landau 2000). In temperate and Mediterranean systems, between 20 and 60% of plant species depend on animals to disperse their seeds (Willson et al. 1990). Therefore, animal-generated seed shadows and the factors conditioning them have been a longstanding topic in ecological research.

However, unraveling which factors drive plant regeneration is particularly challenging because seed dispersal patterns arise from complex interactions between plant and animal traits, animal behavior and the environment (Morales and Carlo 2006, Carlo and Morales 2008, Cortes and Uriarte 2013). In fact, despite the fact that it is well established that environmental conditions can modify seed dispersal effectiveness (sensu Schupp et al. 2010), the behavioral mechanisms underlying such changes remain elusive (reviewed by Cousens et al. 2010). We live in a world with rapidly changing landscapes in which animals are forced to face new conditions of food and habitat availability, local competition for sources and degree of (hostile) matrix permeability to their movements. Under these new conditions animals may move and deposit seeds differently (reviewed by McConkey et al. 2012). Therefore, analyzing seed dispersal from a behavioral perspective will allow for a more realistic assessment of the vulnerability of plants to global change in anthropogenic habitats, for detecting possible causes of seedling recruitment bottlenecks and for developing more adequate management practices.

Mechanistic models of seed dispersal by animals have provided new insights about the nature of seed dispersal kernels, have been used for predicting long-distance dispersal events and also have been crucial in detecting critical gaps in our knowledge of the seed dispersal processes (Westcott et al. 2005, Morales and Carlo 2006, Will and Tackenberg 2008, Morales et al. 2013). They have rapidly evolved from context-dependent models parameterized for specific environmental conditions to new approaches in which seed

shadows emerge as the result of the interplay between the behavior of dispersal agents and the limitations imposed by landscape structure (reviewed by Cousens et al. 2010). Thanks to these new models, it has been possible to assess which environmental factors have major effects on foraging decisions of dispersers and thus modulate seed shadows (Morales and Carlo 2006, Levey et al. 2008, D'Hondt et al. 2012, Bialozyt et al. 2014).

However, to evaluate the effects of land use change on seed dispersal patterns in a dynamic way we need to integrate dispersal with landscape models. This approach translates management decisions into changes in key environmental factors that drive the behavior of seed dispersers. Here we use such an integrated approach to model management effects on the holm oak–rodent mutualism. Holm oak *Quercus ilex* forests are widely distributed in the western Mediterranean basin where they play an important ecological and socio-economic role. Most of these woodlands are highly managed, either by understory removal and tree thinning or by forest fragmentation due to agricultural expansion (Santos and Tellería 1998, Campos et al. 2013). These management practices preclude holm oak recruitment due to dispersal failure and increased seed predation (Santos and Tellería 1997, Pulido and Díaz 2005). In small forest fragments and savanna-like woodlands acorn dispersal mostly depends on wood mice *Apodemus sylvaticus* due to the disappearance of Eurasian jays *Garrulus glandarius*, the main acorn disperser in Europe (Andrén 1992, Bossema 1979, Brotons et al. 2004). However, oak–rodent interaction is not always mutualistic. Depending on environmental conditions, rodents can act as net seed predators or as moderately efficient acorn dispersers (Den Ouden et al. 2005, Gómez et al. 2008). The main drivers of mouse foraging decisions are 1) intraspecific competition for acorns, which is related to direct competition as well as the likelihood of cache pilfering by conspecifics (Theimer 2005, Vander Wall 2010), and 2) the presence of shelter (i.e. shrubs), which determines mouse perception of predation risks while mobilizing acorns (Perea et al. 2011a). Recent observational work has shown that management effects on acorn dispersal quality by rodents can be explained by its effects on these two environmental factors (Morán-López et al. 2015).

An agent based model (ABM) was developed to 1) evaluate the effects of forest management and mouse foraging decisions on acorn dispersal patterns and 2) illustrate the power of mechanistic models as management decision tools. In our model, forest management modifies local intraspecific competition for acorns and shelter availability, and depending on the balance between these two processes mice adapt their foraging strategies, which results in different acorn dispersal patterns. We assume that the main motivation for mice to mobilize and hoard acorns far from mother trees is to store them for winter consumption. For this purpose, mice carry seeds outside areas with high probability of cache pilfering by conspecifics but they do this only tolerating an acceptable amount of predation risk during acorn mobilization. We parameterized our model using pattern orientated modeling on data from one study area. Subsequently we validated it using five independent study sites that included forest interior areas with contrasting stem densities, savanna-like woodlands (dehesa), forest edges and small forest fragments. To assess the effects of mouse foraging decisions and landscape features on acorn dispersal patterns we performed sensitivity analyses.

To illustrate the power of our model as a management decision tool, we simulated acorn dispersal by mice in scenarios of increasing shrub cover in a typical dehesa. Dehesas are savanna-like woodlands used for extensive livestock rearing, which play an important socio-economic role over large areas in the western Mediterranean region (reviewed by Campos et al. 2013). They are also protected by the European Habitats Directive (Ramírez and Díaz 2008). In spite of having been exploited for centuries, limited natural regeneration by oaks threatens the sustainability of dehesas in the long term (Pulido and Díaz 2005, Olea and San Miguel-Ayanz 2006, Díaz 2014). Shrub encroachment has been proposed as an effective and economic way of promoting oak recruitment in this habitat (Ramírez and Díaz 2008, Pulido et al. 2010). Shrubs enhance local mouse abundance and protect seedlings from summer drought and browsing (Smit et al. 2008, Muñoz et al. 2009, Rolo et al. 2013). However, encroachment decreases the economic profitability of the system as it decreases forage production for livestock (Campos et al. 2013). In the light of our simulations results, we evaluated if the minimum shrub cover needed to promote dispersal services provided by mice in dehesas is compatible with their current exploitation.

Material and methods

Field observations

Field data were collected in three study sites of holm oak woodlands of the Iberian Peninsula: in Lerma (northern plateau; 42°5′N, 3°45′W), Quintanar de la Orden (southern plateau; 39°35′N, 3°02′W) and Cabañeros (southern plateau, 39°39′N, 4°28′W). In these three study sites there are six different landscape types. One of these was used for model construction and calibration and the other five for model validation.

Lerma and Quintanar correspond to holm oak archipelagos located in an extensive treeless agricultural region where cereal cultivation has reduced the original forest cover to smaller woodland patches ranging in size between 0.02 and 2000 ha (Santos and Tellería 1998). Field data from these sites were collected in winter 2012–2013 within the framework of an experiment in which fragmentation effects on acorn dispersal by mice were evaluated (Morán-López et al. 2015). Cabañeros is a National Park in which two contrasting landscape configurations can be found, holm oak forests and savanna-like woodlands (dehesas). Dehesas are characterized by a very low stem density (12 trees ha^{-1}) within an open grassland matrix with almost no shrub cover ($< 1\%$). Seed dispersal patterns were measured in winter 2011–2012 in two dehesas (Díaz et al. unpubl.).

In Lerma and Quintanar we monitored acorn dispersal in three fragmentation categories – forest interior areas, forest edges and small fragments. We offered and tracked 405 acorns per locality and fragmentation level (2430 in total). In Cabañeros we tracked 446 acorns. Information on

dispersal patterns included acorn mobilization distances, caching rates and microhabitat selection by mice. Furthermore, field data at the three sites included information of acorn production of oaks, local mouse abundance and understory cover structure. See Morán-López et al. (2015) for further details.

From the observed data we derived information to parameterize directly the effects of holm-oak intraspecific competition on acorn production, the effects of canopy and shrub cover on mouse abundance, in situ predation rates and the probability of depositing a seed under canopy or shrub cover at the end of the mobilization process (Supplementary material Appendix 1: submodels). Additionally, we used the dataset of northern plateau (Lerma) forest edges to determine uncertain model parameters because it contained the largest diversity of landscape structures. The other five datasets (forest interiors of Quintanar and Lerma, forest edges of Quintanar, small forest fragments of both localities and Cabañeros dataset) were used to evaluate the predictive performance of the model.

Modeling approach

To model the effects of landscape management on acorn dispersal by mice, we developed and agent-based model implemented in Netlogo 5.0.4 (Wilensky 1999) a free platform for building ABMs. The Netlogo code is available in supplementary material (Supplementary material Appendix 2). The model description follows the overview and design concepts and details (ODD) protocol for communicating agent-based simulation models (Grimm et al. 2006, 2010). In the following sections, we present the overview and design concepts, for the full ODD protocol see Supplementary material Appendix 1.

Entities, state variables and scales
This ABM comprises five different entities: landscape, trees, shrubs, acorns and mice. The landscape consists of a two-dimensional grid with a cell size of 1 m. It has an area of 5.76 ha, 1 ha in the center corresponding to the study area and a buffer around it of 70 m width (which corresponds to the average home-range radius of *Apodemus sylvaticus* observed in Mediterranean areas; Rosalino et al. 2011) and also to the maximum dispersal distances observed in our study (Morán-López et al. 2015). This buffer avoids artificial edge effects. Each grid cell is characterized by two variables: habitat type (forest or cropland) and microhabitat (open land, shrub or canopy).

Trees are randomly placed within the landscape, but keeping a realistic 4 m minimum distance to each other. Each tree is characterized by its canopy radius and acorn production. Acorns are initially placed on trees and are characterized by the coordinates of their initial and final positions and by their final seed fate ('predated in situ', 'mobilized and predated' or 'dispersed'). Shrubs are randomly placed within the landscape. Mice are randomly placed on the landscape but this placement is constrained by realistic home-range areas and home-ranges overlap (Supplementary material Appendix 1.4.1: Mouse abundance submodel). Then, mice located close to oak trees are allowed to mobilize seeds while the rest of them inform a map of local mouse abundance.

Design concepts, process overview and scheduling
Figure 1 shows how forest management influences the local environmental conditions and how mice adapt their behavior accordingly. From field data we parameterized the effects of landscape structure on acorn production of trees and on local mouse abundance. Acorn production by individual trees in the model is negatively related to intraspecific competition for water resources (Supplementary material Appendix 1.4.1: Acorn production submodel). As a consequence, trees located in areas with lower stem densities or in forest edges surrounded by croplands show higher acorn production. Local mouse abundance is positively related to canopy and shrub cover in forest interiors and it depends on the amount of habitat availability in fragmented areas (Supplementary material Appendix 1.4.1: Mouse abundance submodel). Therefore, the effects of forest management on intraspecific competition for acorns will depend on its net effects on the ratio between local acorn production and mouse abundance (Fig 2A; for further details see Supplementary material Appendix 1.4.1). Finally, open microhabitats represent areas of high predation risks for mice. Thus, our model assumes that landscape permeability to mouse movements depends on the amount of open land cover it has. Depending on forest management effects on intraspecific competition for acorns and the amount of open land cover in the landscape, mouse modify their foraging decisions resulting in different acorn mobilization patterns.

In our model, mouse foraging decisions follow three objectives: 1) mobilize seeds away from potential competitors, 2) avoid moving through risky habitats, and 3) cache seeds in areas where the probability of pilfering by conspecifics is low (Fig. 2B). During the first meters of acorn mobilization mouse decisions are governed by intraspecific competition for acorns. Then, mobilization continues until
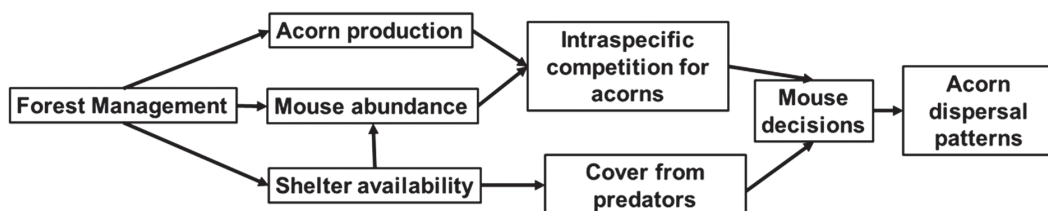

Figure 1. Main processes implemented in the model connecting forest management to acorn dispersal patterns. Forest management modifies local mouse abundance, acorn production and habitat structure, which entails changes in intraspecific competition for acorns as well as availability of cover from predators. Mice modify their foraging strategies according to these new environmental conditions, thereby affecting acorn dispersal patterns.
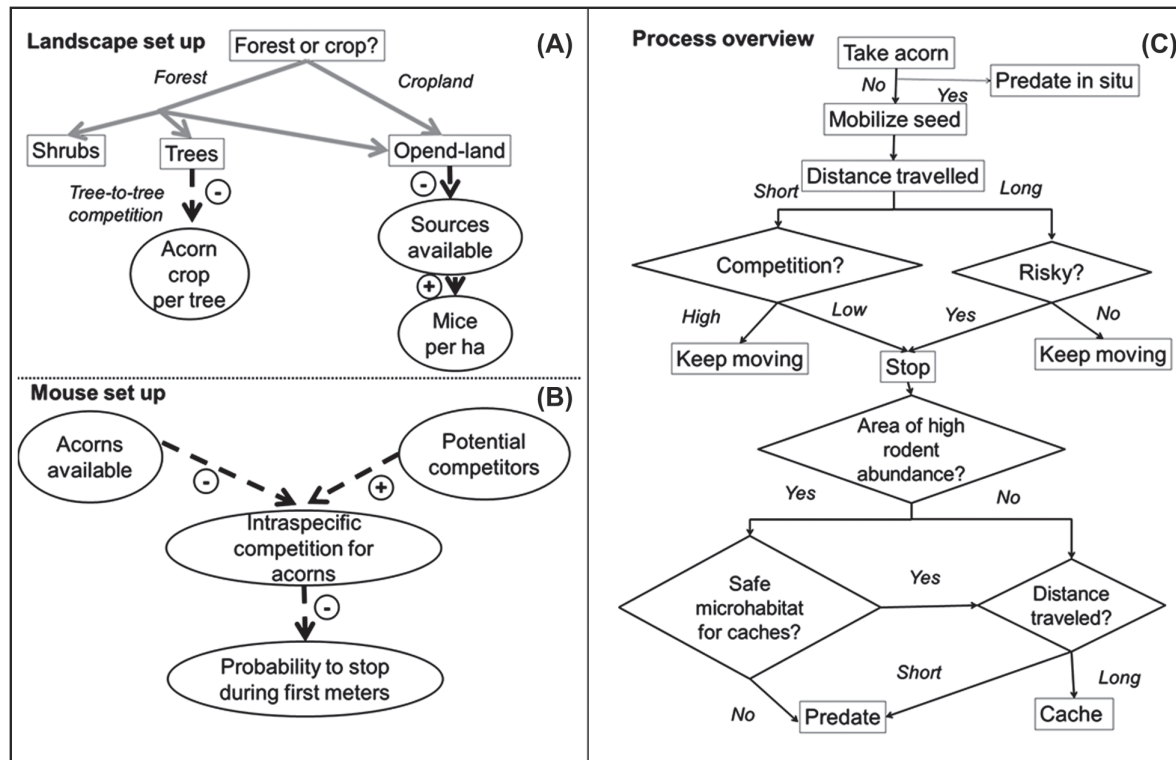
Figure 2. Flow diagrams showing the structure of the model. (A) Procedure to generate landscapes, (B) decision process of mice before starting acorn mobilization, (C) process overview of mouse foraging decisions during mobilization. In (A) grey lines and rectangles represent input values while dashed lines and circles represent parameters that depend on local environmental characteristics. In (C) diamonds depict decision points.

risk perception exceeds a certain threshold. Finally when acorns are deposited, the decision between predation and seed caching depends on the risk of cache pilferage by conspecifics and the effort invested in seed mobilization.

Mouse decisions are made according to three internal variables – intraspecific competition for seeds, competition radius and risk perception. The first two variables represent foraging strategies related to direct competition for acorns and the avoidance of cache pilfering by conspecifics. The third variable defines the amount of risks perceived by mice while mobilizing seeds. Once carried acorns have been deposited, mice return to the source tree and the whole dispersal process restarts. A model run finishes when all acorns within the study area are dispersed (Supplementary material Appendix 1.4.2 for further details).

Initialization – Our model needs three types of input data: proportion of forest habitat loss within the landscape, number of stems per hectare and proportion of shrubs in the understory cover.

Observation – Within the model, acorn mobilization distances as well as their final state (cached versus predated) are recorded (main model output). Caching rates are estimated taking into account in situ acorn predation. Dispersal distances are estimated only taking into account mobilized seeds (acorns predated in situ are disregarded).

Model parameterization

Pattern-oriented modeling was used for model parameterization (Wiegand et al. 2003, Hartig et al. 2011, Railsback and Grimm 2011). We parameterized the model with the data from the results of a field experiment conducted in Lerma in which 405 acorns were tracked in three independent edge areas of large forest fragments (> 100 ha; Morán-López et al. 2015). Four output variables were used for model parameterization, including the maximum dispersal distances, the shape and the rate parameters of a gamma distribution fitted to dispersal distances, and the proportion of cached acorns. A total of 16 000 combinations of parameters were sampled from uniform distributions within biologically plausible ranges for all parameters (Table 1). For each parameter combination, five model simulations were run (variance of mean global values among replicates stabilizes with a sample size of 5). We then estimated global cost of parameter sets. Cost was defined as the sum of the squared relative deviations to the mean value of the acceptable value range over the four different criteria (when model output fell within the acceptable value range its cost was 0; see Thiele et al. 2014 Eq. 1–4). Following an approximate Bayesian computing (ABC) approach, the optimal model parameter combination was then selected from the median of the approximate posterior distributions of parameter sets with low global costs (rejection filter, global cost < 0.15). In the case of risk threshold, the value of maximum frequency was chosen (since this parameter is an integer).

The six parameters estimated were 1) CR, the competition-area radius function, which defines the area in which mouse foraging decisions are governed by intraspecific competition (Eq.4); 2) the parameter PS describing the probability to stop function, that modulates the strength of intraspecific

Table 1. Parameter values estimated during model parameterization and their ranges employed during the sensitivity analysis.

Global process	Process	Sub-process	Parameter	Range during parameterization	Value in base model	Values in sensitivity test
Forest management	–	fragmentation	habitat loss	0.50	–	[0.1, 1]
		forest thinning	stems/ha	400	–	[50, 350]
		understory development	shrub cover	0.25	–	[0.1, 1]
Mouse foraging decisions	acorn mobilization	intraspecific competition effects	competition area radius	[0, 20]	3 m	–
			probability to stop (PS parameter)	[0.10 – 0.60]	0.40	[0.10–0.60]
		predation risk effects	risk perception threshold (N_R)	[0, 4]	1 m	[0, 4]
	predation vs caching	pilfering risk effects	edge-belt width	[0, 60]	35 m	–
		distance travelled effects	maximum caching rates (C1)	[0.5, 1]	0.75	[0.5, 1]
			distance effects (C2)	[0.1, 0.2]	0.16	[0.1, 0.2]

competition effects on mouse foraging decisions (Eq. 5 Supplementary material Appendix 1.4.2, intraspecific competition for acorns submodel); 3) the risk threshold during acorn mobilization (N_R; Supplementary material Appendix 1.4.2: Risk threshold submodel), 4–5) the parameters C1 and C2 describing the caching probability function, which determine maximum caching rates and the strength of the effects of mobilization distances on the probability of acorn caching, respectively (Eq. 7) and 6) edge-belt width, which defines the areas of increased pilfering risks due to increased mouse abundance in forest edges (EW; Supplementary material Appendix 1.4.2: Hoarding versus predation submodel). For further details see Supplementary material Appendix 1.4.2.

The RNetLogo package was used for inverse parameterization (Thiele et al. 2012) following guidelines specified in (Thiele et al. 2014). For fitting the gamma distribution we used the fitdistrplus package (Delignette-Muller et al. 2014).

Model validation

We validated our model with five independent datasets, including forest interiors of the northern plateau (Lerma; n = 3 forest interiors) and the southern plateau (Quintanar; n = 3 forest interiors), forest edges of the southern plateau (Quintanar; n = 3 forest edges), small woodlots within croplands of both plateaus (n = 5 areas of small forest fragments) and Spanish dehesas (n = 2 dehesas). We simulated acorn dispersal by mice based on the optimal model parameterization and on the landscape parameters (habitat availability, stem density and shrub cover) of these study areas. In field data of the northern and southern plateaus each observation corresponds to 135 seeds offered and tracked (Morán-López et al. 2015). In the case of the dehesa 202 and 244 seeds were offered and tracked per observation (Díaz et al. unpubl.). In the case of the Spanish dehesa *Mus spretus* was the main disperser instead of *Apodemus sylvaticus*. Although the model structure remained the same, we needed to adapt the home range radius to 15 m (Gray et al. 1998) and the weight-ratio to 0.24 (field data from Díaz et al. unpubl., Eq. 5 Supplementary material Appendix 1.4.2).

For each landscape we ran 100 independent simulations. To validate acorn mobilization distances we calculated for both observed and simulated data, the mean and the standard error of mean and maximum dispersal distances, the shape and rate parameters of the gamma distribution fitted to dispersal distances, and the distance for 0.95 quantiles. We assumed an acceptable model prediction when mean values of 100 simulations were within the 95% confidence interval of the observed data. We also evaluated the variance explained by the model by regressing observed versus simulated data of the proportion of seeds deposited at a given distance in annuli of 5 m (log-transformed, with a fixed slope of 1) and obtained the R^2.

To evaluate the ability of the model to predict mouse hoarding activity we evaluated if the proportion of cached acorns differed between simulated and observed data. In this case the experimental units were sampled trees instead of forest areas (n = 15 trees for forest interiors and edges, n = 30 for small woodlots). Out of the simulated and observed data we calculated mean and standard errors of caching rates (defined as the percentage of cached seeds). We assumed an acceptable model prediction when the mean values of 100 simulations were within the 95% confidence interval of the observed data.

Sensitivity analyses

Two sensitivity analyses were performed. Firstly, we evaluated the sensitivity of the predicted dispersal pattern to parameters governing mice behavior (decision sensitivity test, hereafter). We used here all parameters that were determined by pattern-oriented modeling (except the edge-belt width EW), landscape scenario corresponded to Northern forest edges (see Table 1 for parameter ranges). In a second analysis we evaluated the net effects of landscape features (landscape sensitivity test, hereafter) based on the standard parameter set shown in Table 1. We varied in this analysis all three parameters used to define a landscape, habitat availability (0.1 to 1), stems per ha (50 to 350), and a proportion shrub cover (0.1 to 1).

We analyzed as output variables the shape and rate parameter of the gamma distribution fitted to the

simulated dispersal kernels, maximum dispersal distances and the percentage of mobilized seeds cached. The shape parameter k describes the location of the maximum probability (k = 1: maximum at x = 0). The rate parameter describes the tail of the dispersal kernel (Var(x) ~ 1/rate^2) lower values imply broader probability distributions with longer tails. This way, we could evaluate which part of the foraging decision process (intraspecific competition, risks assumed during mobilization, or cache pilfering avoidance) influence different aspects of seed dispersal quality (proportion of acorns dispersed close to the mother trees, potential colonization distances and amount of seeds finally cached). To detect linear and non-linear monotonic associations between model parameters being evaluated and output variables, global sensitivity analysis was performed following a partial correlation rank test using sensitivity package in R (Pujol et al. 2014, Thiele et al. 2014). Preliminary plots of the associations between model parameters and model output allowed us to rule out non-monotonic associations (Supplementary material Appendix 3).

Landscape scenarios – dehesa shrub encroachment

To illustrate the potential of ABMs as a tool for the development of adequate management policies we simulated shrub encroachment in a dehesa (savanna-like woodlands with 15 stems per ha) and evaluated its effects on seed dispersal patterns. In particular, its effects on mean and maximum dispersal distances as well as caching rates were evaluated. Preliminary scatterplots showed non-linear responses in the case of mean and maximum dispersal distances. Therefore, the data were fitted to a two parameter exponential growth curve and a four parameter sigmoidal curve (mean and maximum dispersal distances respectively). In the case of caching rates a linear regression was adjusted. Function fitting in all cases was performed using Sigmaplot ver. 12.0 (<www.sigmaplot.com>).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.9nt37> (Morán-López et al. 2016.

Results

Model calibration

ABC parameterization based on the data for forest edges from the northern plateau showed that the model could be parameterized to yield mobilization distances and caching rates patterns close to those of observed data. Regarding mobilization patterns, almost all summary statistics of the simulated data fell within the 95% confidence interval of observed data (Table 2; Northern forest edge, mean and maximum dispersal distances, rate parameter, quantile of probability 0.95). The model slightly underestimated the proportion of seeds that were deposited in the first 5 m (Fig. 3A) and the shape parameters of the gamma distributions fitted to dispersal distances were slightly higher than those of the observed data (Table 2). However, there was a general good agreement between observed and simulated data (R^2 = 0.88 fit between log-transformed data of observed and expected seed deposition at a given distance). Besides, caching rates fell within the 95% confidence interval of observed data (Table 3, Northern forest edge).

Model validation

Our parameterized model predicted acorn dispersal distances (Fig. 3, Table 2) and caching rates (Table 3) that agreed well with the data from the five independent landscape scenarios tested. Our model yielded similar acorn mobilization patterns than those observed in Southern forest edges (Fig. 3B, Table 2, R^2 = 0.88, between log-trans-

Table 2. Model parameterization and model validation. The data from the northern forest edges were used for model parameterization, all other dataset were used for model validation. The table shows summary statistics of seed dispersal distances of observed and simulated data. Values of observed data correspond to 95% confidence interval. Values of simulated data represent mean ± SE. Mean = mean dispersal distance, max = maximum dispersal distance, shape = shape parameter of gamma distribution fit, rate = rate parameter of gamma distribution fit, 0.95 = distance for quantile of probability 0.95. Northern and Southern forests correspond to Lerma and Quintanar datasets respectively, small forest fragments correspond to dataset of both localities and Dehesa corresponds to Cabañeros National Park dataset.

Landscape	Type	Mean	Max	Shape	Rate	0.95
Northern forest edge**	observed	[1.00, 4.90]	[9.88, 53.07]	[0.50, 0.57]	[0.10, 0.18]	[4.26, 25.38]
	simulated	4.35 ± 0.06	44.03 ± 0.93	0.63 ± 0.00	0.15 ± 0.00	6.78 ± 0.30
Southern forest edge	observed	[1.25, 3.42]	[23.70, 38.15]	[0.58, 0.73]	[0.17, 0.45]	[4.80, 20.86]
	simulated	2.69 ± 0.02	26.07 ± 0.70	0.77 ± 0.07	0.29 ± 0.04	8.73 ± 0.17
Northern forest interior	observed	[4.77, 10.63]	[34.63, 71.33]	[0.51, 0.64]	[0.04, 0.13]	[17.02, 35.90]
	simulated	4.10 ± 0.05	45.63 ± 1.03	0.62 ± 0.04	0.15 ± 0.00	15.32 ± 0.27
Southern forest interior	observed	[1.25, 4.16]	[16.15, 39.37]	[0.46, 0.75]	[0.07, 0.50]	[4.83, 23.03]
	simulated	2.19 ± 0.03	14.46 ± 0.34	0.90 ± 0.01	0.42 ± 0.04	5.86 ± 0.05
Small fragment	observed	[1.43, 2.60]	[6.37, 13.85]	[0.86, 1.20]	[0.37, 0.77]	[4.21, 8.4]
	simulated	2.00 ± 0.01	14.61 ± 0.61	2.83 ± 0.05	1.42 ± 0.03	4.37 ± 0.03
Dehesa	observed	[0.98, 1.26]	[2.95, 7.12]	[1.96, 2.43]	[1.52, 2.42]	[2.44, 2.76]
	simulated	1.63 ± 0.02	7.20 ± 0.11	1.81 ± 0.25	1.13 ± 0.17	3.68 ± 0.11

*The simulated data consist on 100 independent model runs. In forest interiors and forest edges field data consist on three indepent dispersal kernel estimations (offered seeds = 135 in each observation). For small forest fragments field data consist on five independent kernel estimations (offered seeds = 135 each observation). In dehesa, field data consist on two independent estimation of dispersal kernels (offered seeds = 202 and 244)**Dataset used for inverse modeling parameterization
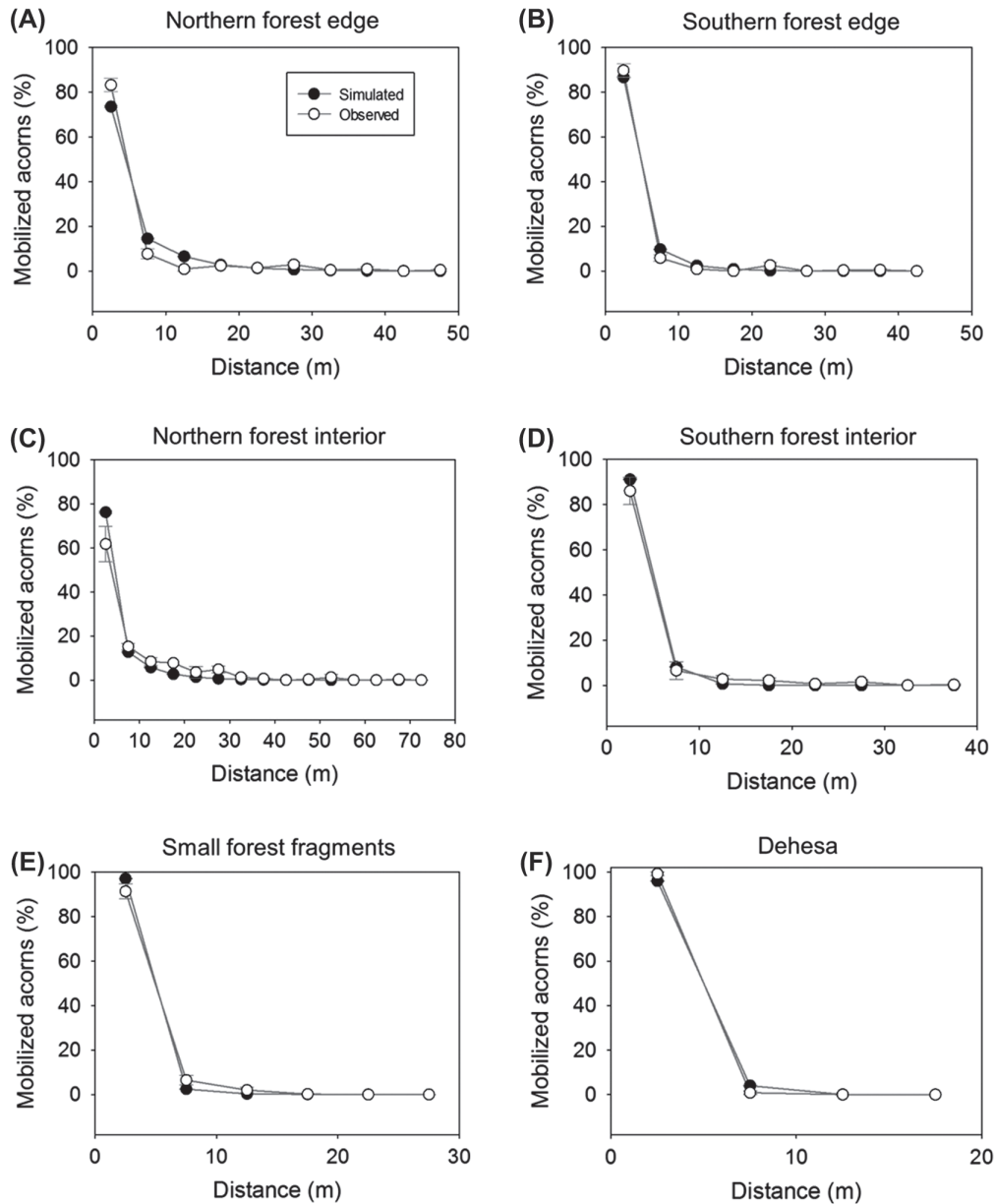
Figure 3. Comparison of seed dispersal kernels from simulated (black, filled circles) and observed (open circles). The simulated data consist on 100 independent model runs. In forest interior and edges field data consist on three independent dispersal kernel estimations (offered seeds = 135 in each observation). For small forest fragments field data consist on five independent kernel estimations (offered seeds = 135 each observation). In dehesa, field data consist on two independent estimation of dispersal kernels (offered seeds = 202 and 244). Northern and Southern forests correspond to Lerma and Quintanar datasets respectively, small forest fragments correspond to dataset of both localities and Dehesa corresponds to Cabañeros National Park dataset. Bars represent 95 confidence intervals.

formed data of observed and expected seed deposition at a given distance, slope fixed to 1). In northern forest interiors, our model overestimated short-range mobilization distances (0–5 m; Fig. 3C). However, the fit between observed and expected seed deposition at a given distance was high ($R^2 = 0.95$). Furthermore, predicted mean and maximum dispersal distances, dispersal kernel parameters and the distance corresponding to for 0.95 quantile of the probability all fell within the 95% confidence interval of observed data (Table 2). Simulated data for Southern forest interiors accurately reproduced field-observed patterns (Fig. 3D, $R^2 = 0.91$, Table 2). Although the fit between

observed and simulated data was high for small forest fragments ($R^2 = 0.99$, Fig. 3E), the proportion of seeds deposited close to the source point was overestimated and kernel tails were thinner (shape and rate parameter, Table 2). Finally our model was able to reproduce the field data of the dehesa accurately (Fig. 3F, Table 2, $R^2 = 0.99$). In all cases the mean values of the simulations caching rates fell within the 95% confidence interval of observed data (Table 3). However, mean values of caching rates in small forest fragments were in the lower limit of the confidence interval and caching rates in dehesas were in the upper limit.

Table 3. Model parameterization and model validation - summary statistics of mice hoarding activity of observed and simulated data. Data represent the percentage of mobilized seeds that were cached by rodents. Values of observed data correspond to 95% confidence interval. Values of simulated data represent mean ± SE. Northern and Southern forests correspond to Lerma and Quintanar datasets respectively, small forest fragments correspond to dataset of both localities and Dehesa corresponds to Cabañeros National Park dataset.

Landscape	Type	Cached acorns
Northern forest edge**	observed	[3.65, 13.70]
	simulated	9.46 ± 0.23
Southern forest edge	observed	[2.4, 10.03]
	simulated	5.91 ± 0.14
Northern forest interior	observed	[11.03, 22.72]
	simulated	15.19 ± 0.26
Southern forest interior	observed	[2.40, 17.12]
	simulated	8.18 ± 0.15
Small forest fragments	observed	[2.25, 7.07]
	simulated	2.35 ± 0.11
Dehesa	observed	[0, 1.83]
	simulated	1.84 ± 0.14

*Field data corresponding to forest interiors and edges consist on 15 trees located in three indepent locations (offered seeds = 27 per tree). For small forest fragments field data consist on 30 trees located in 16 independent small woodlots (offered seeds = 27 per tree). In dehesa, field data consist on two indepent dehesas (offered seeds = 202 and 244 per dehesa). **Data used in inverse modeling parameterization.

Sensitivity analysis

Model parameters driving mouse foraging decisions were correlated differently to short-range mobilization patterns, maximum mobilization distances and caching rates (Fig. 4). In general, seed dispersal distances were sensitive to both the importance of intraspecific competition on acorn mobilization (parameters CR and PS) and the predation risks accepted by mice during acorn mobilization (parameter NR). However, the relative importance of the parameters CR, PS and NR differed between dispersal kernel estimates and maximum dispersal distances. The shape and rate parameters of the kernels were most strongly correlated to the CR and PS parameters (Fig. 4A–B) and the shape and rate parameters of the dispersal kernel increased when both parameters increased. These results fit our expectation that mice tend to mobilize seeds closer to the parent tree when intraspecific competition effects are relaxed. This translates into dispersal kernels characterized by higher probabilities of mobilization events close to the source point as well as shorter and thinner tails (higher shape and rate parameters).

However, maximum dispersal distances were mainly correlated with predation risks accepted during mobilization (parameter NR; Fig. 4C). When mice accepted a higher risk the landscape matrix became more permeable to mouse
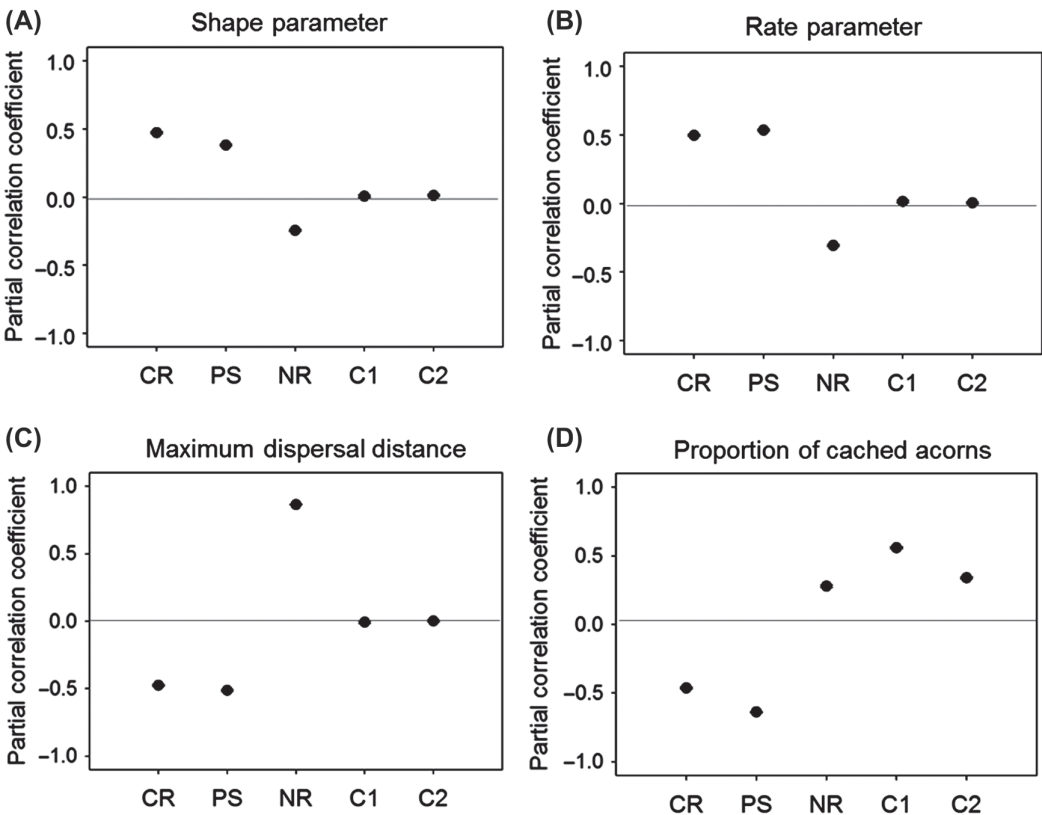

Figure 4. Sensitivity analysis of mouse foraging decisions. Results show the partial rank correlation (PRCC) between mouse foraging decisions parameters and the following model output variables: (A) the shape and (B) the rate parameter of the gamma distribution fitted to mobilization distances, (C) maximum dispersal distance, and (D) proportion of cached acorns. Circles represent PRCC values. Bars that indicate bootstrapped (n = 100) 95% confidence intervals corresponding to sensitivity indices are eclipsed by the symbols. CR: competition radius (Supplementary material Appendix 1.2, Eq. 4); PS: parameter of probability to stop function (Supplementary material Appendix 1.2, Eq. 5) , NR: risk-treshold giving the maximal number of consecutive movement steps in the risky open land, C1: maximum caching rates with distance, C2: effects of distance on the probability of acorn caching (Supplementary material Appendix 1.2, Eq.7).

movements and hence maximum mobilization distances increased.

Shape and rate parameters of dispersal kernels were more robust to changes in model parameters than maximum dispersal distances. This is due to the fact that kernel estimates collect information about all mobilization events; hence, changes in these parameters imply great differences in overall mobilization patterns.

Caching rates were related to all decision points, however, they were correlated to a greater extent to the parameters PS and the maximum caching rate (C1) (Fig. 4D). The former result is in accordance to our expectation that mice invest higher efforts in safeguarding acorns for winter consumption as the effects of intraspecific competition increase. The second is simply related to the maximum of the caching probability function (Eq. 7, Supplementary material Appendix 1.2).

Landscape sensitivity analysis (Fig. 5) revealed that forest habitat loss is a key factor for seed dispersal quality. Higher habitat loss was related to overall shorter mobilization distances (shape, rate parameters) as well as lower caching rates. Shrub cover was highly correlated to maximum dispersal distances. Stem density showed the lowest effects on all parameters except for caching rates. Thus, our landscape sensitivity analysis revealed that parameters related to changes in both intraspecific competition for acorns and matrix permeability, had greater effects on acorn mobilization distances and caching rates.

Landscape scenarios – dehesa shrub encroachment

Shrub encroachment effects in a typical dehesa produced non-linear responses for dispersal distances. The two parameter exponential curve and the three parameter sigmoidal curve fitted well our simulations of shrub encroachment effects on mean and maximum dispersal distances (Fig. 6A–B, $R^2 = 0.89$; $R^2 = 0.96$, respectively). In both cases, shrub encroachment effects did not become evident until shrubs represented between a 50 and a 65% of understory cover. In the case of caching rates, encroachment effects became evident straight away. However, caching rates did not reach a 10% until shrub cover was greater than a 40% (Fig. 6C). In summary, our results show that shrub encroachment has minor effects on seed dispersal quality if understory shrub cover is below 40% and that these effects do not become evident until shrubs represent more than a 65% of the understory cover.

Discussion

Animal-generated seed shadows in human-modified woodlands emerge from complex interactions between management effects on environmental conditions and animal behavior (Cortes and Uriarte 2013). Here, we analyzed the effects of land-use changes on acorn dispersal patterns
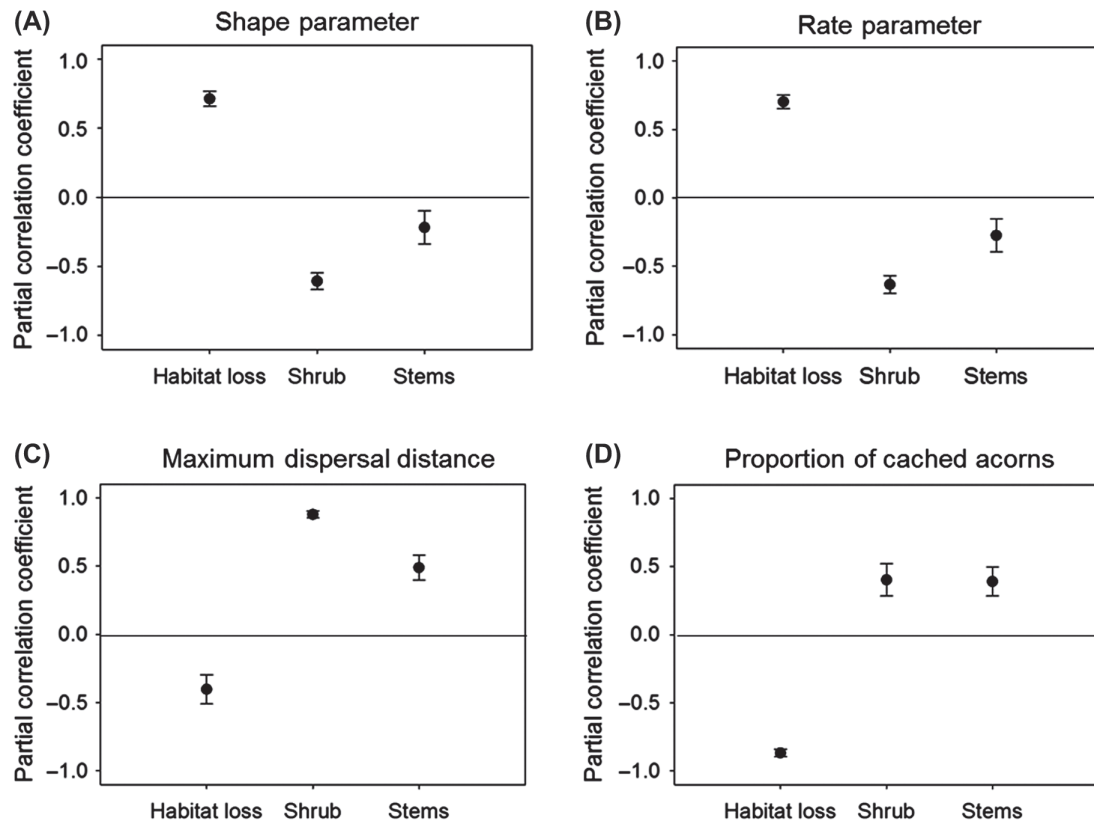

Figure 5. Sensitivity analysis of landscape parameters. Results show the partial rank correlation (PRCC) between landscapes attributes and the following model output variables: (A) the shape and (B) the rate parameter of the gamma distribution fitted to mobilization disances, (C) maximum dispersal distance, and (D) proportion of cached acorns. Circles show PRCC values and sticks show bootstrapped (n = 100) 95% confidence intervals corresponding to sensitivity indices. Landscape parameters: forest habitat loss (%), shrub cover (proportion) and stems per ha.
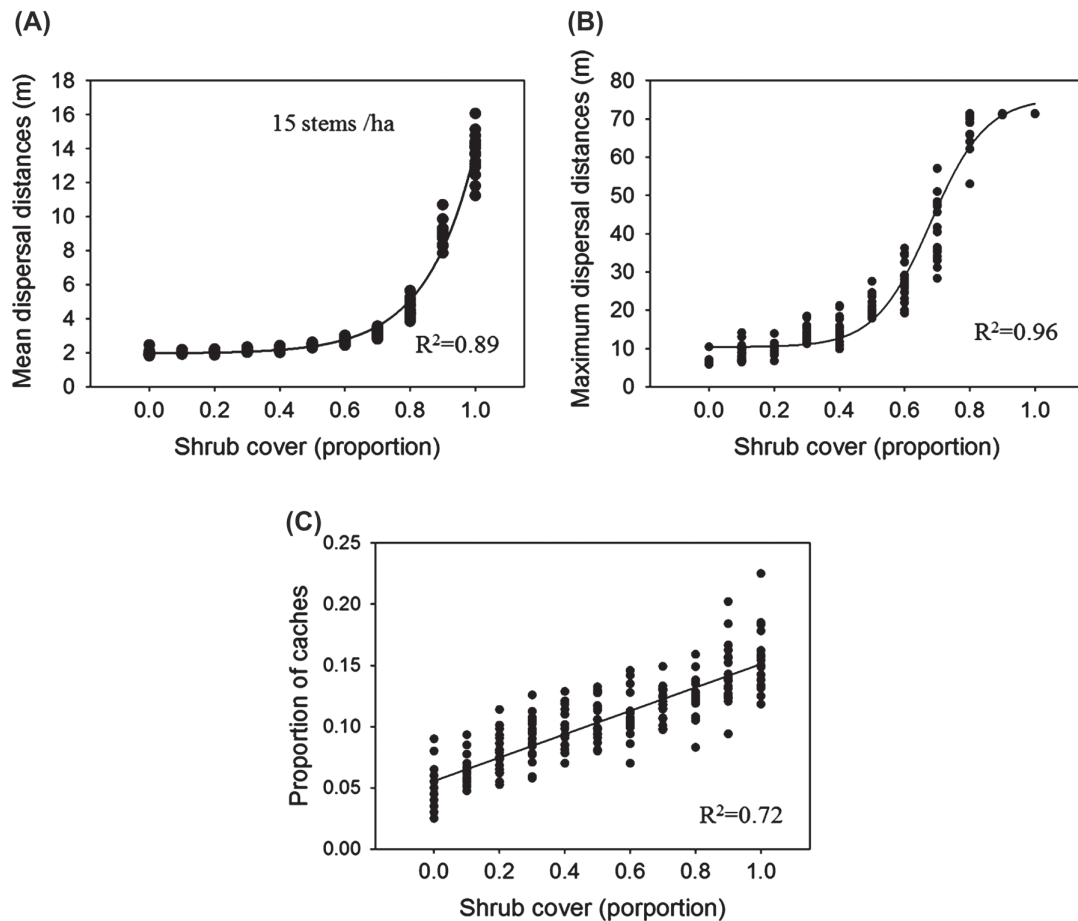
Figure 6. Model predictions of dehesa shrub encroachment effects on: (A) mean dispersal distances (fitted curve; $= 0.33 \times e^{3.64x}$); (B) maximum dispersal distances (fitted curve; $y = 10.35 + 65.08/1 + e^{(-x-0.68)/0.09)}$) and (C) caching rates (fitted curve; $y = 0.05 + 0.10x$). Points represent model output, lines represent fitted curve.

in holm oak woodlands using an approach that integrates forest management effects on key environmental factors for rodents with their subsequent foraging decisions. Previous work on holm oak woodlands from different perspectives, including acorn production, mouse population dynamics and oak–rodent mutualisms provided an understanding of the mechanisms that potentially drive acorn dispersal patterns (Valladares et al. 2014). Including these processes into our model allowed us to reproduce simultaneously several key features of acorn dispersal patterns in a variety of forest management scenarios that were not used for model parameterization. Furthermore, successful application of a slightly modified model version to dehesa landscapes where acorns are dispersed by *Mus spretus* (instead of *Apodemus sylvaticus*) showed that the model incorporates general decision processes of rodent species since the same environmental factors seem to modulate their foraging behavior (Theimer 2005, Vander Wall 2010).

Effects of mouse foraging decisions on seed dispersal patterns

Sensitivity analysis has helped in previous modeling work to disentangle the behavioral mechanisms behind the main attributes of seed dispersal kernels (Morales and Carlo 2006,

Bialozyt et al. 2014). Our 'decision sensitivity test' aimed at identifying those foraging decisions with greater effects on different aspects of seed dispersal quality. This approach allowed us to interpret large-scale management effects on seed rain patterns from a behavioral perspective.

Our results showed that a higher proportion of acorns were deposited closer to the mother tree when the effects of intraspecific competition for seeds were relaxed. This result is in accordance with previous observational work (Puerta-Pinero et al. 2010, Morán-López et al. 2015). As pointed out by Moore et al. (2007), when resources are abundant, rodents depend less on the stored food and pilfering pressure decreases. In such cases, optimal cache distances are determined by minimizing energy costs rather than by minimizing cache pilfering risks resulting in shorter mobilization distances and higher clumping of caches. In contrast, maximum dispersal distances mainly depended on the risks assumed by mice while mobilizing seeds. This is in agreement with the idea that maximum dispersal distances are largely determined by matrix permeability to seed-vector movement (Schurr et al. 2008). In general, animals reduce their mobility and forgo certain foraging opportunities as predation risk increases (Brown 1992; reviewed by Verdolin 2006 and Creel and Christianson 2008). The same applies to rodents (Banks et al. 2002, Haapokoski et al. 2015). In

particular, wood mice are known to avoid areas frequented by predators (Díaz et al. 2005, Navarro-Castilla and Barja 2014) as well as open microhabitats (Muñoz et al. 2009, Perea et al. 2011a). In fact, studies monitoring individual movements have found that home ranges shrink when exposure to predation increases (Tew and Macdonald 1993, Tattersall et al. 2001). Regarding foraging behavior, wood mice invest less effort in food selection and manipulation in risky environments than in safe ones (Perea et al. 2011b). In our model, the landscape matrix became more permeable, and consequently dispersal distances increased, when mice perceived lower predation risks or took riskier decisions.

The aim of scatter-hoarders is to store seeds for winter consumption and, hence, rodents act as dispersers only when seed caches escape retrieval or pilfering (Den Ouden et al. 2005). In general, seed dispersal models focus on how environmental factors modulate animal movement and the effects of seed handling are rarely taken into account (reviewed by Cousens et al. 2010, but see D'Hondt et al. 2012). However, when modeling oak–rodent mutualistic relationship the difference between seed caching and predation needs to be included. In fact, initial caching rates in forest habitats ranges from 7 to 40 percent and seed survival until late autumn from 9 to 20 percent (Gómez et al. 2008, Perea et al. 2011a, Morán-López et al. 2015). As pointed out by our sensitivity analysis, caching rates emerge from the interplay between intraspecific competition for seeds and the risks taken during mobilization. There was a good agreement between predicted and observed values in all landscape scenarios, which suggests that the main drivers of seed caching by wood mice were included in the model. When intraspecific competition for seeds is high mice carry seeds far from the mother tree and cache them in areas where the risk of pilfering by conspecifics is relatively low (Den Ouden et al. 2005, Gómez et al. 2008, Puerta-Piñero et al. 2010, Perea et al. 2011a).

Management effects on seed dispersal patterns

Mice were able to adapt their behavior to environmental conditions, resulting in different seed dispersal patterns that were similar to field observations. Forest habitat loss had a great effect on seed dispersal kernels as well as on caching rates. When habitat loss occurs two processes take place, intraspecific competition is relaxed and landscape becomes less permeable to mice movements. Despite the fact that local mouse abundance is higher at forest edges (García et al. 1998), increments in acorn production are much higher resulting in lower intraspecific competition for acorns (Morán-López et al. 2015). As a result, rodents invest less effort in moving and caching seeds (Moore et al. 2007). Besides, in fragmented areas predation risks incurred by mice when moving across croplands are particularly high (Tew and Macdonald 1993). Therefore, as habitat loss progresses the benefits of safeguarding caches from competitors by mobilizing seeds outside forest fragments decline and acorn predation rather than caching becomes the dominant strategy (Morán-López et al. 2015). Shrub cover was tightly related to maximum dispersal distances, and to a lesser extent to shape and rate parameter of the dispersal kernel. In the light of the 'decision sensitivity test', shrub encroachment effects on shape and rate parameters may be mediated by its positive effects on local mouse abundance and hence intraspecific competition for acorns. In contrast, its effects on maximum dispersal distances would be mediated by mouse perception of lower predation risks while mobilizing seeds. Likewise, in field studies shrub cover has been found to enhance acorn mobilization distances (Morán-López et al. 2015).

Landscape scenarios – shrub encroachment of dehesas

Our model predicted that a high proportion of shrub cover is needed (65%) in order to restore dispersal distances and caching rates. Shrub cover below this threshold would be almost ineffective due to non-linear responses. In our model, mice acted as seed dispersers only when local mouse abundance and matrix permeability increased greatly in dehesas. This may result from a very low intraspecific competition for seeds due to the large acorn production of trees. Minimum shrub cover predicted by our model may not be compatible with the human exploitation of dehesas since it would dramatically decrease pasture productivity (main food source for livestock in autumn and spring; Moreno and Pulido 2007). In agreement with previous work, our results suggest that lack of regeneration is an inherent feature of grazed dehesas (Pulido et al. 2001, Plieninger et al. 2003, Pulido et al. 2010). Furthermore, these results support the idea that rotation strategies ensuring the presence of undergrazed or livestock-excluded plots should be implemented in order to guarantee the natural regeneration of dehesas (Moreno and Pulido 2007, Ramírez and Díaz, 2008, Díaz 2014). However, livestock income might be replaced by public subsidies to overcome landowners' reluctance to reduce their stocking rates (Moreno and Pulido 2007, Campos et al. 2013). To develop adequate government policies, estimating the time needed to ensure natural regeneration is of paramount importance. Modeling approaches that include dispersal and demographic processes in relation to management options will provide very useful information in this regard.

Model limitations and caveats

During simulations mice mobilize seeds following a correlated random-walk depositing acorns along a preferential direction. However, the choice of such direction is random. Previous observational work suggests that wood mice deposit seeds in clumped patterns and it has been suggested that enhanced mobilization distances are related to lower aggregation of caches (Puerta-Piñero et al. 2010). Therefore, mobilization distances could be reflecting both aspects of seed dispersal quality. Nonetheless, it is unlikely that rodents select a preferential direction of seed mobilization irrespectively of habitat characteristics. For instance, in agro-forest systems wood mice preferentially use habitats that ensure food acquisition or encounters with potential mates (Rosalino et al. 2011). Collecting new data that combine tracked mice during the fruiting period and seed deposition patterns are needed to find out if wood mice use preferential seed dispersal paths in highly heterogeneous landscapes. Such data may allow us to parameterize a more realistic movement model that can create anisotropic two dimensional maps

of the probability of seed dispersal (Santamaría et al. 2007, Rodriguez-Perez et al. 2012).

For the sake of simplicity, our model used randomly distributed shrubs and did not include microhabitat effects on seedling recruitment. However, microhabitat of acorn deposition has important effects on post-dispersal predation and seedlings dry out, main bottlenecks for acorn-seedling survival in Mediterranean areas (Gómez 2004, Smit et al. 2008). Seed-sowing experiments in different management scenarios that include information about local mouse abundance and acorn production will help to easily include seedling recruitment in the model.

Conclusions

We developed a model that translates management decisions into environmental changes that drive mouse foraging behavior. With this integrated approach we assessed which foraging decisions modulate different attributes of acorn dispersal services provided by mice and the behavioral mechanisms underlying forest management effects on such services. Our model was able to predict acorn dispersal patterns in a wide range of management scenarios with a few empirical variables. In fact, the only input variables required by the parameterized model are the proportion of forest habitat within the landscape, the density of stems and the cover of shrubs.

However, despite that recruitment cannot occur without seed arrival, seedling establishment also depends on post-dispersal process like post-dispersal seed predation, seedling survival to summer drought or seedling intraspecific competition (Wang and Smith 2002). Therefore, future work that estimates clumping of dispersed acorns and microhabitat effects on final seed fate will help to evaluate to what extent changes in seed dispersal patterns are reflected in the demographic structure of oak populations.

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Supplementary material (available online as Appendix oik-02884 at <www.oikosjournal.org/appendix/oik-02884>). Appendix 1–3.