

# Short seed-dispersal distances and low seedling recruitment in farmland populations of bird-dispersed cherry trees

Nils Breitbach<sup>1,2,3\*</sup>, Katrin Böhning-Gaese<sup>2,3,4</sup>, Irina Laube<sup>1,2,3</sup> and Matthias Schleuning<sup>2,3</sup>

<sup>1</sup>Institut für Zoologie, Johannes Gutenberg-Universität, Abteilung 5: Ökologie, D-55128, Mainz, Germany; <sup>2</sup>Biodiversität und Klima Forschungszentrum (BiK-F), Senckenberganlage 25, D-60325, Frankfurt a. M., Germany; <sup>3</sup>Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, D-60325, Frankfurt a. M., Germany; and <sup>4</sup>Department of Biological Sciences, Goethe-Universität Frankfurt am Main, Max-von-Laue-Straße 9, D-60438, Frankfurt a. M., Germany

## Summary

1. In Central Europe, many plant populations are patchily distributed in human-modified landscapes and depend on animal vectors for seed dispersal. To predict seed-dispersal distances and locations of seeds of wild cherry trees (*Prunus avium* L.) in forest and farmland habitats in a human-modified landscape, we integrate movement data and seed regurgitation times of the Common Blackbird (*Turdus merula* L.) in a simulation model.

2. We performed feeding trials with Common Blackbirds and wild cherries to determine the distribution of regurgitation times. We captured 32 male blackbirds and equipped them with radio tags to follow their movements in forest and farmland habitats. To simulate the movement of cherry seeds through the landscape, we combined the distribution of regurgitation times with bird movement data and modelled seed-dispersal distances and locations of seed deposition for forest and farmland birds.

3. According to our simulations, more cherry seeds were deposited under foraging trees in farmland (20.8%) than in forest populations (9.5%). Median seed-dispersal distances (50.8 vs. 68.2 m) and the proportion of long-distance dispersal events (distances > 100 m) were predicted to be lower in farmland (14.9%) than in forest populations (28.2%).

4. In the model, forest-dwelling blackbirds dispersed more cherry seeds into suitable habitat (98.7%) than farmland blackbirds (85.4%). In both habitats, seed deposition in suitable habitat was much higher than expected from the proportion of suitable habitat within blackbirds' home ranges, indicating directed dispersal.

5. To test whether differences in seed-dispersal locations were related to recruitment success, we recorded seedling densities in farmland and forest populations of *P. avium* and determined survival probabilities of seedlings. Seedling densities and survival were much lower in farmland than in forest populations, even accounting for strong environmental effects on seedling recruitment.

6. **Synthesis:** Our findings show that behavioural differences of animal seed dispersers between habitat types can result in substantial changes in seed-dispersal distances and locations in human-modified habitats. These changes in seed-dispersal services for bird-dispersed plant species may be related to reduced seedling recruitment in farmland populations making such populations prone to extinction in the long term.

**Key-words:** animal movement, ecosystem function, land-use intensity, mutualism, plant-animal interactions, *Prunus avium* L., seed dispersal, seedling recruitment, *Turdus merula* L., VHF radio telemetry

## Introduction

Human-modified landscapes dominate most terrestrial ecosystems around the globe (Millennium Ecosystem Assessment

\*Correspondence author. E-mail: nils.breitbach@senckenberg.de

(MEA) 2005; Tylianakis *et al.* 2008). In temperate regions, human land-use intensification has been particularly strong and agricultural landscapes have experienced substantial modifications (Foley *et al.* 2005; Millennium Ecosystem Assessment (MEA) 2005; UNEP 2007). These processes have created isolated patches of semi-natural habitats within an intensively utilized agricultural matrix, which has important consequences for the dynamics of plant (Cain, Milligan & Strand 2000; García & Chacoff 2007) and animal populations (Howe & Miriti 2004; Tylianakis, Tschamtko & Lewis 2007).

Plant populations in intensively used landscapes are usually patchily distributed (Franzén & Nilsson 2010). Many plants depend on animal vectors, often birds, for the movement of their seeds among these habitat patches (Snow & Snow 1988; Levey *et al.* 2005; Jordano *et al.* 2011). Birds can act as 'mobile links' between plant populations and transport seeds over long distances through unfavourable habitats and can, hence, interconnect isolated plant populations (e.g. Lundberg & Moberg 2003; Breibach *et al.* 2010; García, Zamora & Amico 2010). Previous studies have found that flight and thus dispersal distances were longer in structurally simple agricultural landscapes than in forest (Gómez 2003; Lenz *et al.* 2011).

So far, many studies have investigated seed dispersal only in terms of dispersal distance (e.g. Holbrook & Smith 2000; Westcott & Graham 2000; Westcott *et al.* 2005; Lenz *et al.* 2011). However, from the plants' perspective, it is not only important how far seeds get dispersed but also where seeds are finally deposited (Schupp, Jordano & Gómez 2010). The 'Directed Dispersal Hypothesis' (*sensu* Howe & Smallwood 1982) predicts that animal vectors can increase the probability that seeds are transferred to sites with suitable conditions for plant recruitment (Wenny 2001), thereby increasing recruitment success (Wenny & Levey 1998). Directed dispersal is particularly important in human-modified landscapes where suitable habitats are patchily distributed (Cain, Milligan & Strand 2000; García & Chacoff 2007) and where many seeds are prone to be dropped into the unsuitable habitat matrix (Schupp 1993; Cain, Milligan & Strand 2000; Nathan 2006; Schurr, Steinitz & Nathan 2008). Consequently, seed deposition in suitable habitats is expected to be lower in landscapes where suitable habitats are patchily distributed, such as farmland, than in homogeneous forests (Dunford & Freemark 2004; Westcott *et al.* 2005; García, Zamora & Amico 2010).

A valuable approach to assess how seed-dispersal services by birds change along a land-use gradient is to combine movement data of animal dispersal vectors, for example, from radio tracking, with their gut retention time of seeds (Westcott *et al.* 2005; Lenz *et al.* 2011). Movement data and retention times can be integrated in predictive models of the distribution of seed-dispersal distances provided by animal vectors. However, previous studies using this approach did not incorporate habitat requirements of the studied plant species into their model (Westcott & Graham 2000; Spiegel & Nathan 2007; García, Zamora & Amico 2010; Lenz *et al.* 2011; Karubian *et al.* 2012) and thus did not account for seed fate after dispersal which ultimately translates into recruitment success (Schupp, Jordano & Gómez 2010). Hence, there is a

lack of studies that have linked predicted patterns of seed deposition with estimates of plant recruitment, such as seedling recruitment and survival (but see McConkey & Brockelman 2011). We therefore know little about how seeds are distributed in human-modified landscapes and how patterns of seed deposition translate into plant recruitment success.

In this study, we integrate movement data and seed regurgitation times of the Common Blackbird (*Turdus merula* L.) in a simulation model to predict seed-dispersal distances and locations of seeds of wild cherry trees (*Prunus avium* L.) in forest and farmland habitats in a human-modified landscape. The wild cherry is one of the most widespread bird-dispersed tree species in Central Europe; blackbirds are the most important seed dispersers of many woody species in this region (Snow & Snow 1988; Breibach *et al.* 2010). We recorded in a previous study that birds remove wild cherry seeds at similarly high frequencies in forest and farmland habitats (Breibach *et al.* 2010). However, we do not know how seed-dispersal distances and locations change along the forest-farmland gradient. We therefore analysed movement behaviour of blackbirds in forest and farmland and combined these data with regurgitation times of wild cherry seeds. Our main objectives were to model distributions of seed-dispersal distances of wild cherries in forest and farmland habitats and to predict probabilities of seed deposition in habitats suitable for seedling recruitment. We related the findings of the model to the observed patterns of seedling recruitment of wild cherries in forest and farmland. We tested the following hypotheses: (i) seed-dispersal distances are longer in farmland than in forest because we expected longer flight distances of blackbirds in farmland than in forest. (ii) The probability of seed deposition in suitable habitat is higher in forest than in farmland where suitable habitats are more patchily distributed. To test whether these potential differences in seed dispersal were related to recruitment success, we compared seedling recruitment of wild cherries between forest and farmland habitats.

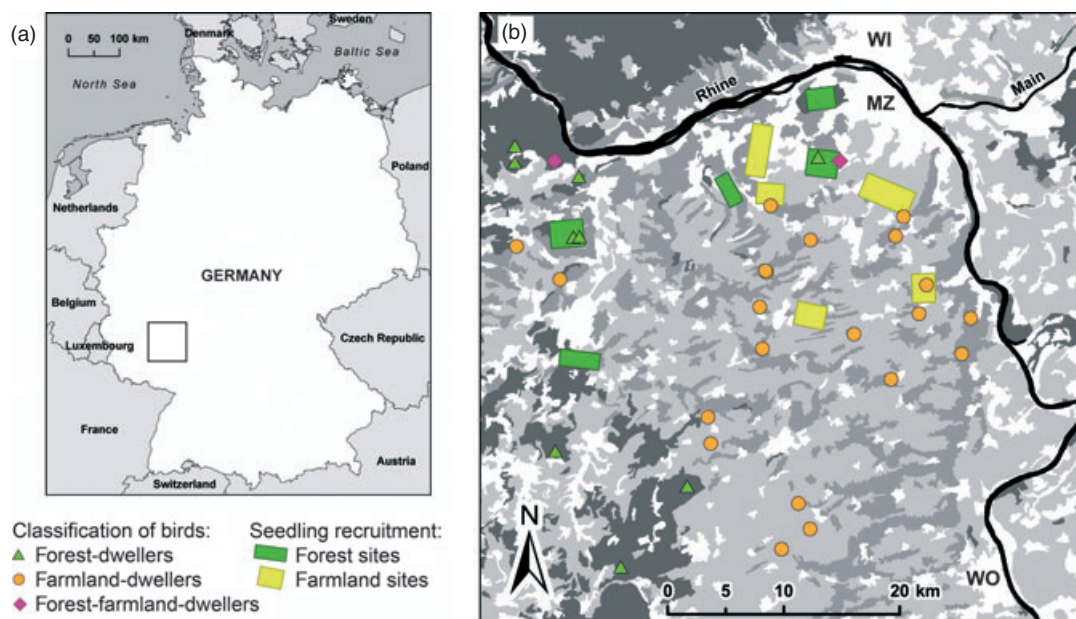
## Materials and methods

### STUDY REGION

Our study region is located in Rhineland-Palatinate (49°38' N–49°58' N, 7°45' E–8°22' E) in Central Germany and covers approximately 1900 km<sup>2</sup> (Fig. 1). The region belongs to one of the warmest and driest parts of Central Europe (mean annual temperature: c. 10.0 °C; average rainfall: 500 mm; Ambos & Kandler 1987). The central part of the study region is intensively used for agriculture (grain, wine, rape-seed, vegetables and some pomiculture), interspersed with patches of semi-natural habitat such as transitional woodland shrub, pastures, natural grasslands and sparsely vegetated areas. It is surrounded by mountain ranges in the north-west (Hunsrück, Taunus) and south-west (Donnersberg) that are covered with mixed deciduous forest.

### STUDY SPECIES

The wild cherry, *P. avium* L. (Rosaceae), is a widespread tree and inhabits a broad range of different habitats including deciduous mixed forest, forest edges, small woods, hedgerows and fallows. *Prunus*



**Fig. 1.** Map of the study area: (a) Location of the study area in Central Germany, indicated by a square. (b) The location of 32 Common Blackbird home ranges in the study area. Courses of main rivers are shown in black (i.e. Rhine and Main); larger cities abbreviated as WI (Wiesbaden), MZ (Mainz) and WO (Worms). Also shown are forests (dark grey shaded areas), viniculture and pomiculture (middle grey shaded areas) and structurally simple agricultural landscapes (light grey shaded areas).

*avium* is a small deciduous tree growing up to 15–20 m in height. The species flowers in April and May; the fruiting period lasts from June to August (Breitbach *et al.* 2010, 2012). The fruits consist of a fleshy mesocarp that turns from green to glossy black during ripening and a single seed encased in a wooden endocarp (i.e. a drupe). Fruits are roundish with a diameter of  $14.7 \pm 2.2$  mm (mean  $\pm$  1 SD,  $N = 1,674$ ) and weigh  $2.0 \pm 1.0$  g (mean  $\pm$  1 SD,  $N = 1,674$ ). Ripe cherries are consumed and dispersed by birds and mammals (Breitbach *et al.* 2010; Grünwald, Breitbach & Böhning-Gaese 2010). Seeds of wild cherry trees require winter stratification and germinate in the spring of the following year prior to foliation of deciduous trees (Suszka, Muller & Bonnet-Massimbert 1996).

The Common Blackbird (*T. merula* L., blackbird hereafter) is one of the most abundant and widespread frugivores in Europe (Bauer, Bezzel & Fiedler 2005) and is the main disperser of wild cherry seeds in our study area (Breitbach *et al.* 2010). Blackbirds inhabit a wide range of different habitat types from dense forest, woodland, structurally complex to structurally simple agricultural landscapes and urban areas (Haffer 1988). Individuals inhabiting different habitat types differ in behaviour and habitat use and are genetically differentiated (Partecke, Van't Hof & Gwinner 2004). For our study, we selected only male birds, which are more important for cherry seed dispersal as most females breed during the fruiting period of wild cherry trees and hence move only short distances.

#### FEEDING TRIALS

We captured 15 adult male blackbirds at the University Campus in Mainz in early summer of 2009 and 2010. The wild birds were held separately in cages of  $1 \times 1 \times 2$  m (length  $\times$  width  $\times$  height). We performed feeding trials with all captured birds using fresh ripe wild cherries from trees within our study area. Blackbirds swallow wild cherry drupes as a whole and later regurgitate the seed. Thus, wild cherry fruits, unlike smaller fruits, do not pass through

the birds' gut. We never observed any regurgitation event while the birds were in flight; the process of regurgitation involves a suffocate movement that appears to be impossible in flight. All caged birds had access to food (fat-enriched bird food, mealworms, fruits other than cherries) and water before and throughout the feeding trials to get the best approximation to an *ad libitum* feeding and digesting situation. To be able to determine the exact regurgitation time (RT) for a particular seed, we offered only one cherry drupe per feeding trial. For each feeding trial, we calculated the RT as the time span from the time of ingestion to the time of regurgitation, that is, when the seed dropped to the floor of the cage. We fitted an average RT distribution (function 'density' in R) across all feeding trials ( $N = 63$ ; mean = 4.2; range 2–7 trials per bird individual) with a bandwidth of 5 min as a smoothing factor. This approach allowed us to predict the proportion of seeds that were regurgitated during 1-min intervals within the range of observed regurgitation times (see Fig. S1-1, Appendix S1 in Supporting Information). We also fitted three parametric distributions to the observed regurgitation times, that is, lognormal, Gamma and Weibull (see Fig. S1-1 in Appendix S1), and used the function 'fitdist' from the R package 'fitdistrplus' to calculate log-likelihood, AIC, BIC and estimates for each parametric distribution as measures for the goodness-of-fit (see Tables S1 and S2 in Appendix S1).

#### RADIO TRACKING AND MOVEMENT ANALYSIS

We caught 32 adult male blackbirds with mist-nets in both forest and farmland habitats (Fig. 1) in two consecutive field seasons in June and July 2009 and 2010 (eight and 24 birds, respectively). All birds were individually marked with a unique combination of three colour rings to allow for reliable visual identification of each bird in the field. We supplied all birds with VHF radio tags (PIP3, Biotrack Ltd, Wareham, UK) using the leg-loop harness method (Rappole & Tipton 1990; Naef-Daenzer 2007). The average tag weight of 2.3 g (total payload = 2.6 g) was well below the threshold of 5% of the birds'

body mass (Kenward 2001). We used single filaments of braided rubber ropes (Mamutec AG, St. Gallen, Switzerland) as leg-loops which allowed tags to fall off after about 12 weeks. We started radio tracking 1 week after birds had been captured so that birds were able to adapt to the tag before radio tracking started.

Tracking took place in June and July 2009 and 2010, during the fruiting season of the wild cherry. We followed the study birds continuously from sunrise (about 5:20 h) to sunset (about 21:40 h). We located the birds in the early morning using a portable telemetry multichannel receiver (Telonics TR-4; Telonics Inc., Mesa, AZ, USA) in combination with an H-antenna (Telonics RA-14). During bird-tracking, we recorded a new location and the duration of the time spent at each location whenever we recognized a change in the birds' position; we never recorded locations while the birds were in flight because we focused on locations of potential seed uptake or seed deposition. Our aim was to obtain visual contact with the bird as often as possible. In cases in which we did not see the bird, we used the antenna to estimate a birds' location from signal strength and direction. To record the location of the bird, we either measured the location of the bird directly after the bird had left the position using a GPS receiver (Garmin eTrex Vista HCx, Deutschland GmbH, Garching, Germany) or fine scale maps. Alternatively, we recorded the observer position using the GPS receiver, measured the bearing and the distance from the observer to the bird (using a laser range finder; Nikon Laser800S, Nikon GmbH, Düsseldorf, Germany) and later computed the location of the bird using the function 'gcDestination' in the R package 'maptools' (Lewin-Koh & Bivand 2011). The use of these methods enabled us to track the birds without chasing or flushing them. In this manner, we finally knew where birds stayed and for how long and we were thus able to obtain the location of each bird with a temporal resolution of one minute; in total, we collected 103 742 locations (range of tracking days and locations per bird: 1–11 days and 438–6229 locations,  $N = 32$  birds).

To quantify the availability of suitable habitats for wild cherry trees at potential seed-deposition sites, we determined the habitat type at the position of each location using GIS software (ArcGIS v. 10.0, Environmental Systems Research Institute (ESRI) Inc., Redlands, CA, USA). For habitat classification, we used digital land-use data from our study area (ATKIS Basis-DLM 2011; spatial resolution  $\pm 3$  m). We manually added missing information, for instance, narrow hedgerows in structurally simple landscapes. Habitat types defined as potentially suitable for seedling recruitment of wild cherry trees were broad-leaved and mixed forest (*not* coniferous forests), woods, woodland shrub, hedgerows and green belts at road verges (see Table S2-1 in Appendix S2). All other habitat types were defined as unsuitable. We did not discriminate potential differences in habitat quality among suitable habitat types. We placed buffer zones of 10 m radius around the coordinate of each bird location. All bird locations that included one of the suitable habitat types inside the buffer zone were classified as potentially suitable locations for wild cherry establishment. Buffering each location with a 10 m radius takes into account that habitat conditions at habitat margins (e.g. at the forest edge) are likely to be suitable for seedling recruitment and also accounts for cumulative inaccuracies of GPS locations and GIS data.

#### MODELLING SEED-DISPERSAL DISTRIBUTIONS

To assess potential dispersal distances and locations of cherry seeds, we combined the distribution of regurgitation times (Fig. S1-1 in Appendix S1) with bird movement data of all tracking days of an individual bird (following e.g. Westcott *et al.* 2005; Lenz *et al.*

2011). We first drew 10 000 time intervals from the RT distribution (with replacement). For instance, a RT of 30 min had a probability of 3.52% and was therefore approximately 352 times included within the total of 10 000 regurgitation times (Table S1-3 in Appendix S1). The movement data for each individual bird were arranged as a list of records containing all bird locations over the whole tracking period at which the bird was recorded together with the respective time for that record to finally obtain one record for every minute of available data; the list of records contained only stop-over locations (no locations where the birds were in flight) and thus only these locations were available for the following modelling procedures. We then drew 10 000 random starting points (i.e. the time of a record) from the movement data of each individual bird, applied the respective regurgitation time, determined the bird's location at the time of potential regurgitation and measured the distance between the starting point and the location of potential regurgitation; note that this distance is not the movement distance of a bird but the distance for the direct connection between the potential ingestion and potential regurgitation location. Because we aimed at modelling the potential dispersal of wild cherry seeds, we defined that seed-dispersal events could only start while the bird was located in a habitat type that was potentially suitable for wild cherry trees. In cases in which no endpoint (i.e. the time of the second drawn record) could be matched with the respective starting point and given time interval, a new starting point was drawn for that time interval. For each bird, we calculated the distribution of potential dispersal distances (Fig. S3-1 in Appendix S3) by dividing dispersal distances into evenly distributed distance classes on a logarithmic scale (i.e. 0.2 units on a  $\log_{10}(x + 1)$ -scale) and calculating the mean percentage of seed-dispersal events ( $\pm 1$  SE) in each distance class. We chose a logarithmic scale because distributions of seed-dispersal distances resembled a lognormal distribution.

We calculated the average seed-dispersal distribution of the wild cherry across the 32 blackbirds. To account for the varying number of locations among bird individuals, we weighted individuals by the  $\log_{10}$  of the total number of recorded locations. Birds with more locations were thus given more weight compared to birds with a lower number of locations. This procedure resulted in an overall seed-dispersal distribution for our study area. To assess the efficiency of wild cherry seed dispersal, we split the distribution of seed-dispersal distances into dispersal events into suitable habitats for the wild cherry and dispersal events into unsuitable habitat. We did this for each bird individual separately (Fig. S3-2 in Appendix S3) and then averaged across all bird individuals.

To assess habitat-specific seed dispersal, we compared seed dispersal by blackbirds between forest and farmland. We classified the 32 bird individuals as either forest or farmland birds by identifying the ATKIS categories that belong to forest or to farmland (Table S2-2 in Appendix S2) and calculating for each bird individual how frequently a bird was located in forest or in farmland. Most birds showed strong habitat preferences for either forest or farmland. For nine blackbirds, more than 85% of their locations were situated in forest, for 21 birds more than 80% of their locations were recorded in farmland (Table S4-3 in Appendix 4). Only two of the 32 birds were recorded with similar frequencies in forest and farmland (Table S4-3 in Appendix 4) and were therefore excluded from the analysis of habitat-specific seed dispersal. Hence, for the following analyses, nine blackbirds were classified as forest birds and 21 blackbirds were birds predominantly foraging in farmland. We only allowed starting points of seed-dispersal events that were located in the respective habitat type, that is, we selected from forest birds only movement tracks that started in forest and for farmland birds only in farmland. We then

used the same procedure as described earlier to estimate the distributions of seed-dispersal distances for blackbirds of forest and farmland and estimated the proportion of seeds that were deposited into either suitable or unsuitable habitat.

We compared whether the modelled proportion of regurgitation events directly at the potential foraging tree, that is, null-dispersal events, differed between forest and farmland birds. Additionally, we compared median dispersal distances (excluding null-dispersal events) between forest and farmland birds. To assess potential long-distance dispersal events, we defined long-distance dispersal as dispersal events > 100 m distant from the foraging tree (*sensu* Cain, Milligan & Strand 2000), determined the proportion of these events for each blackbird and compared the proportions between forest and farmland birds.

Finally, we tested whether blackbirds engage in directed dispersal of cherry seeds into suitable habitats or distribute seeds randomly across all habitat types within their potential foraging ranges. To do so, we compared the predicted proportion of seed-dispersal events into suitable versus unsuitable habitat types with the availability of suitable and unsuitable habitat types within the foraging range of each bird individual. We first calculated 100% minimum convex polygons (MCPs) and the corresponding areas from the locations of each individual bird using the function 'mcp' included in the 'adehabitatHR' R package (Calenge 2006). We then used ArcGIS to determine the proportions of suitable and unsuitable habitat inside each MCP through intersection with the ATKIS data. Suitable habitat types included a 10-m buffer zone around all habitats that are potentially suitable for seedling recruitment; this approach is consistent with habitat classifications of potential seed-deposition sites. Separately for blackbirds in forest and farmland, we then tested whether the proportion of suitable habitat for wild cherry trees within the foraging range of a bird differed from the proportion of predicted dispersal events into suitable cherry habitat.

#### SEEDLING DENSITY AND SURVIVAL

In 2009, we selected five sites in forest habitats (at least 50 m from the forest edge) and five farmland sites, that is, hedgerows and small woods, with wild cherry populations (Fig. 1). At each site, we established five study plots that had a pair-wise distance of at least 150 m. Study plots cut through a cherry population, that is, were suitable cherry habitats and were 100 m long and 2 m wide (plot size 200 m<sup>2</sup>). Within each plot, we counted all cherry seedlings at the beginning and in the middle of April when cherry seedlings just had established. Cherry seedlings are readily identified by the shape of their first leaves and can be distinguished from cherry saplings or clonal offspring by the presence of cotyledons. The number of seedlings at the first and the second count was closely correlated ( $N = 50$ ,  $r = 0.98$ ,  $P < 0.001$ ). We therefore only compared the number of seedlings during the second census between forest and farmland sites.

To assess whether seedling survival differed between forest and farmland, we selected at each site the study plot with the highest number of seedlings and individually marked all cherry seedlings within the respective plot with straw rings and numbered tags in mid-April. At sites with many seedlings, we did not mark all of them but randomly selected 20 seedlings; the number of marked seedlings per site ranged from 4 to 20 seedlings. We followed the fate of these seedlings until mid-June in 2-week intervals and checked at each census whether a seedling was still alive. Seedling survival was the proportion of marked seedlings that had survived the entire census period until mid-June. This survival rate is a good proxy for first-year seedling survival because the mortality of cherry seedlings from June

to September was very low in a previous study (M. Schleuning, unpublished data). Differences in seedling mortality between forest and farmland sites were tested in a generalized linear model with a binomial error distribution (function 'glm').

To record environmental conditions in each plot, we took five random samples of the upper soil layer (depth 5 cm). At each sampling point, we also measured the depth of the litter layer. To determine soil water content, we weighed a mixed soil sample per plot on the same day and again after 24 h of drying at 105 °C. From the same soil samples, we determined the nitrogen content with an element analyser (Vario EL cube, Elementar Analysensysteme GmbH, Hanau, Germany). To estimate the relative light availability in each plot, we measured photon flux on the ground with a Quantum sensor (LI-191, LI-COR, Lincoln, NE, USA) at six equally spaced points in each plot. At the same time, we determined ambient light availability with another sensor (LI-190) under full light exposure in the open landscape. Relative light availability was then determined as the ratio of the two measurements and was averaged across repeated measures within the same plot. We analysed effects of environmental conditions and of habitat type on seedling recruitment in a generalized mixed-effect model with a Poisson error distribution (function 'glmer' in 'nlme' R package; Pinheiro, DebRoy & Sarkar 2009). We included site ( $N = 10$ ) and, to account for over-dispersion, plot ( $N = 50$ ) as random factors in the model. Fixed effects (i.e. litter layer, soil water content, soil nitrogen content, relative light availability and habitat type) were stepwise removed from the full model (backward elimination,  $P > 0.05$ ).

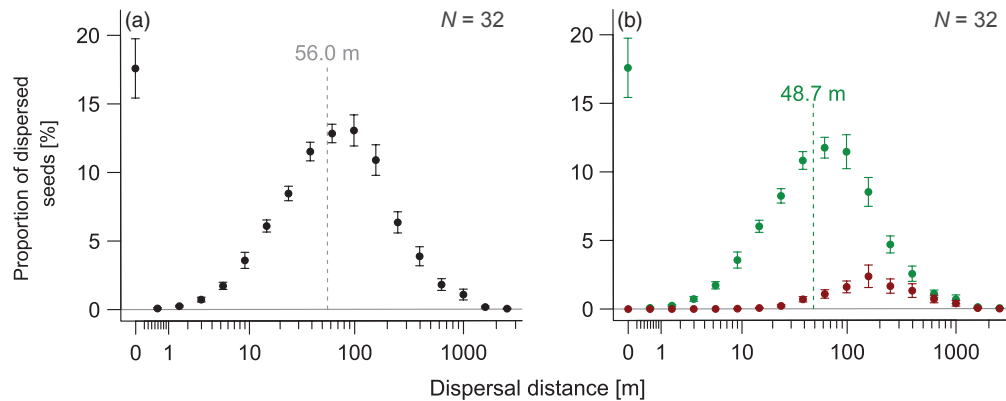
## Results

#### FEEDING TRIALS

Regurgitation times (RTs) of cherry seeds in 63 feeding trials ranged from 8 to 98 min with a median of 30 min (Fig. S1-1 in Appendix S1). The distribution of RTs was leptokurtic with a peak at around 29 min and a fat tail to the right. The lognormal distribution fitted the data better than Gamma and Weibull distributions ( $\Delta AIC = 4.6$  to the next best function; compare Table S1-2 in Appendix S1) and visually resembled the density estimation (compare bold curves in Fig. S1-2 in Appendix S1). We used the density estimation for our simulation model because it reflected the observed distribution of RTs most accurately (compare fits in Fig. S1-1 in Appendix S1).

#### OVERALL DISTRIBUTION OF SEED-DISPERSAL DISTANCES

A considerable number of seeds (mean = 17.6%, range = 2.3–59.1%,  $N = 32$  birds) were modelled to be deposited at the foraging tree and were thus not dispersed (null-dispersal, i.e., dispersal events with dispersal distance = 0 m; Fig. 2a). Median predicted seed-dispersal distance was 56.0 m (Fig. 2a; range: 11.4–133.4 m; Fig. S3-1 in Appendix S3). According to the model, 28.2% of the seeds (range: 5.9–60.0%) were expected to be dispersed > 100 m from the foraging tree with a maximum potential seed-dispersal distance of 2220 m. The proportion of seeds predicted to be deposited in suitable habi-



**Fig. 2.** Predicted seed-dispersal distances (SDDs) for the cherry-blackbird system. (a) Overall SDDs averaged over all 32 blackbird individuals ( $\pm 1$  SE). (b) SDDs of (a) were split into seed-dispersal events into suitable habitat for the wild cherry (green curve) or unsuitable habitat (red curve). For each curve (except the red curve), the median of the SDD is indicated (dashed line). Note the high proportion of seeds that were not dispersed away from the place of origin (i.e. null-dispersal events) at the left-hand side of each distribution.

tat for the wild cherry was 89.9% (Fig. 2b). In our model, seed deposition in unsuitable habitat was negligibly small at dispersal distances  $< 50$  m and was relatively more important at large distances.

#### HABITAT-SPECIFIC SEED-DISPERSAL DISTANCES

According to the model, null-dispersal from the potential foraging tree was significantly more frequent in the farmland (20.8%) than in the forest (9.5%; unpaired Wilcoxon test:  $W = 41$ ,  $P = 0.014$ ; Fig. 3a,b). In contrast to our hypothesis, the model predicted that blackbirds in forest dispersed seeds over longer distances than birds in farmland. Even when neglecting null-dispersal events, median dispersal distances were significantly longer in forest (68.2 m) than in farmland (50.8 m; unpaired Wilcoxon test:  $W = 153$ ,  $P = 0.007$ ; Fig. 3a,b). The proportion of long-distance seed-dispersal events ( $> 100$  m) was calculated to be twice as high in forest (28.2%) than in farmland (14.9%; unpaired Wilcoxon test:  $W = 163$ ,  $P = 0.001$ ). However, the predicted maximum seed-dispersal distances for forest (774.0 m) and for farmland birds (998.8 m) did not differ between the two habitat types (unpaired Wilcoxon test:  $W = 72$ ,  $P = 0.326$ ).

#### DIRECTED DISPERSAL IN FOREST AND FARMLAND

The model predicted that forest-dwelling blackbirds dispersed almost all cherry seeds into suitable habitat (98.7%), whereas blackbirds in farmland sites deposited a significantly smaller proportion of seeds into suitable habitat (85.4%; unpaired Wilcoxon test:  $W = 168$ ,  $P < 0.001$ ). We compared these predicted proportions with the proportion of suitable habitats that were available within the home ranges of blackbirds in forest and in farmland. Potentially suitable habitat types for wild cherries accounted for 87.5% of habitat types within home ranges of forest-dwelling blackbirds compared to a much lower proportion of only 18.0% for blackbirds that inhabited farmland (unpaired Wilcoxon test:  $W = 186$ ,  $P < 0.001$ ;

Fig. 3c,d left bars). In both habitat types, the predicted seed deposition in suitable habitat was much higher than would be expected from the available proportion of suitable habitat (paired Wilcoxon tests: forest:  $V = 45$ ,  $P < 0.004$ , Fig. 3c; farmland:  $V = 231$ ,  $P < 0.001$ , Fig. 3d), indicating that potential seed-deposition sites were not placed randomly in the home ranges of blackbirds. All statistical analyses were conducted in R 2.14 (R Development Core Team 2011).

#### SEEDLING DENSITY AND SURVIVAL

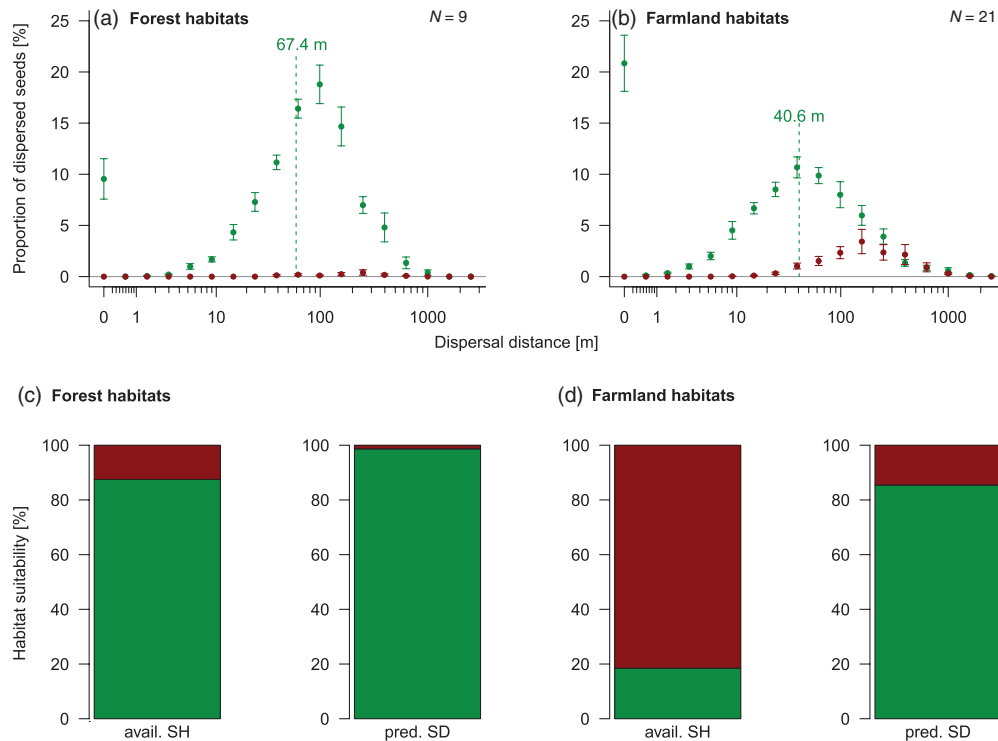
Density of cherry seedlings decreased with the depth of the litter layer and increased with soil water content and relative light availability (Table 1); soil nitrogen content had no effect. In addition to these environmental effects, seedling density was significantly higher in forest than in farmland habitats (mean number of established seedlings in forest versus farmland habitat: 14.6 vs. 4.9 seedlings per plot; Table 1). Differences in seedling recruitment between habitat types further increased during the vegetation period because seedling survival was twice as high in forest (33.3%) than in farmland habitats (15.4%;  $z = 2.03$ ,  $P = 0.043$ ; residual deviance = 2.98). Substantially higher recruitment success of wild cherry seedlings in forest habitats, even after accounting for environmental differences between habitats, was consistent with longer and more directed seed dispersal by blackbirds in forest than in farmland habitats.

## Discussion

#### SEED-DISPERSAL DISTANCES

Our model predicted that blackbirds disperse wild cherry seeds differently in forest and farmland habitats. These results are consistent with the findings of previous studies, which showed that movement patterns of birds change along habitat gradients in human-modified landscapes (e.g. Gómez 2003; Spiegel & Nathan 2007; Lenz *et al.* 2011). Most previous studies have





**Fig. 3.** Seed-dispersal distributions (SDDs; *graphs*) and directed dispersal capacity (*barplots*) for Common Blackbirds in forest and farmland habitats. SDDs for (a) forest habitats ( $N = 9$  forest-dwelling blackbirds) and (b) farmland habitats ( $N = 21$  farmland-dwelling blackbirds). For each SDD curve, the predicted SDDs ( $\pm 1$  SE) into suitable (*green*) and unsuitable (*red*) habitat for wild cherries are given. For each *green* curve, the median of the SDD is indicated (*dashed line*). Differences between the proportion of available suitable habitat (*avail. SH*; in%) and predicted seed deposition (*pred. SD*; in %) in (c) forest habitats and in (d) farmland habitats with *green* representing suitable habitat and *red* indicating unsuitable habitat for wild cherries.

found that movement and dispersal distances increased in structurally simple landscapes (Graham 2001; Gómez 2003; Nathan *et al.* 2008; Lenz *et al.* 2011). In the cherry-blackbird system, we found, however, more frequent null-dispersal events, shorter median seed-dispersal distances and fewer long-distance dispersal events in farmland than in forest.

A likely explanation for this pattern could be the smaller home ranges of blackbirds in farmland than in forest

(Hanauer 2010). Food sources, for example, fruiting trees, are highly aggregated in the farmland, for instance, in hedgerows, and are more evenly distributed in the forest (Breitbach *et al.* 2012). Similarly, microhabitats for foraging for insects and for resting are more clumped in farmland and more evenly distributed in forest. Simulation models of bird movements show that seed-dispersal distances depend strongly on the spatial aggregation of resources (Morales & Carlo 2006). In general, clumped spatial distributions of resources lead to smaller home ranges of the dispersers and shorter dispersal distances (Morales & Carlo 2006). Another explanation for the difference between our results and previous studies might be that the blackbirds in our study were breeding and territorial, whereas most previous studies have investigated the movement patterns of less territorial bird species or non-breeding individuals (Holbrook & Smith 2000; Graham 2001; Gómez 2003; Holbrook 2011; Lenz *et al.* 2011). The movement behaviour of territorial and non-territorial species differs widely. For instance, Sun *et al.* (1997) have found that territorial turaco species have much smaller home ranges than non-territorial turaco species in an African forest ecosystem. Thus, seed-dispersal distances provided by birds may strongly differ among bird individuals depending on the time of the year and the breeding status of each particular individual.

A further explanation for the differences in results to previous studies (e.g., Nathan *et al.* 2008; Lenz *et al.* 2011) might

**Table 1.** Determinants of seedling recruitment of wild cherries in the study area

Source of variation	<i>b</i>	SE	<i>z</i>	<i>P</i>
Litter layer	−0.37	0.117	−3.16	0.002
Soil water content	0.08	0.026	2.93	0.003
Light availability	3.80	1.417	2.68	0.007
Habitat type (forest)	0.80	0.220	3.63	< 0.001

Minimal adequate model of the effects of environmental conditions and habitat type on seedling densities in 50 study plots at 10 sites equally distributed in forest and farmland habitats. Model estimates *b* and standard errors SE as well as test statistic *z* and *P*-values are given for fixed effects; soil nitrogen content was excluded ( $P > 0.05$ ). Study plot and study site were included as random effects in the generalized mixed-effects model ('Poisson' error distribution). The residual deviance of the minimal adequate model was 87.5.

be variation among bird species in their behavioural responses to heterogeneous landscapes and habitat boundaries. In the blackbird-cherry system, 30 of the 32 bird individuals were restricted mostly to forest or mostly to farmland and only two individuals frequently moved between forest and farmland habitats. According to our simulations only about 0.6% of the cherry seeds were transported from farmland into forest and vice versa. Correspondingly, differences in behaviour and microhabitat use and even genetic differences were found for blackbirds in different habitats (Partecke, Van't Hof & Gwinner 2004). In contrast, other bird species frequently cross-habitat boundaries (e.g. Da Silva, Uhl & Murray 1996; Eshiamwata *et al.* 2006; Herrera & García 2009) and are important for an exchange of seeds between plant populations (Pejchar *et al.* 2008; Herrera & García 2009).

#### DIRECTED DISPERSAL

In the farmland, fewer seeds were predicted to reach potentially suitable habitats than in the forest. Nevertheless, despite the low proportions of suitable habitat in the farmland (18.0%), blackbirds deposited the majority of cherry seeds in suitable habitats such as hedgerows and woodlots (85.4%). This strong directed dispersal effect is due to the fact that blackbirds prefer locations with woody vegetation cover and avoid open agricultural habitats such as cropland. In the forest, almost all cherry seeds (98.7%) were deposited in suitable habitats, although foraging ranges of blackbirds in the forest contained considerable proportions of unsuitable habitat, mostly patches of coniferous forests (up to 17.5%). Thus, blackbirds provide directed dispersal into suitable habitat in both habitat types. Blackbirds regurgitated all cherry seeds. As regurgitation takes place only while the bird is perched and not while in flight, this further increases the likelihood that seeds are deposited in suitable habitat. In contrast, larger bird species often defecate seeds after gut passage, even those of large-sized fruits (Snow & Snow 1988; Lenz *et al.* 2011), which is also possible in flight. The difference between regurgitation and defecation has direct implications for the efficiency of seed dispersal, as regurgitation reduces the number of seeds that are dropped en route, that is, on the way from one suitable habitat patch to another. Species-specific handling of seeds can thus lead to more directed seed dispersal to suitable habitats. High rates of directed dispersal, also in other plant-bird dispersal systems, may explain why hedgerows and small woodlots have been identified as dispersal foci for fleshy-fruited trees in human-dominated landscapes (Berens *et al.* 2008; Pejchar *et al.* 2008; Herrera & García 2009).

#### SEEDLING RECRUITMENT

Densities and survival of cherry seedlings were much higher in forest than in farmland populations. This difference persisted after accounting for strong environmental effects on seedling recruitment (Table 1). We propose that the unexplained differences in seedling recruitment between forest and farmland populations are likely to be caused by differences in

seed-dispersal services by birds between habitat types. A possible explanation is that a higher proportion of cherry seeds were deposited in unsuitable habitat in farmland than in forest and that less seeds reached suitable habitat in farmland than in forest. However, seed rain is similar in forest and farmland populations at our study sites (Breitbach *et al.* 2010). Therefore, it seems plausible that the differences in dispersal distances are the main determinant of the higher recruitment probabilities in forest than in farmland, as establishment probabilities are in general higher for seeds that have been dispersed over longer distances (Nathan & Muller-Landau 2000). This is because seedling mortality is usually higher close to parental plants because of higher densities of specialized pathogens and herbivores in dense conspecific stands (Janzen 1970; Connell 1971; Schupp, Jordano & Gómez 2010). Farmland populations of wild cherries have very high adult densities, whereas adult trees are less clumped in forest habitats (Böhm 2009). Clumps within the farmland are often a result of clonal propagation from root stocks (Fernandez, Santi & Doufour 1996) and may consist of a single or a few different clones. It seems likely that cherry seeds have to be transported beyond such clumps because intra-specific competition with competitively superior clonal propagules can strongly reduce seedling recruitment in clonal plant populations (Schleuning, Huamán & Matthies 2009). In our system, we found that the proportion of damaged leaves, probably by fungi infections, increased with the density of adult cherry trees in a population ( $N = 10$  populations,  $r = 0.69$ ,  $P = 0.026$ ; Böhm 2009). Therefore, short dispersal distances in the farmland that usually do not reach beyond a clump of adults may contribute to low recruitment of cherry seedlings in dense farmland populations.

The consistent patterns in seed-dispersal distances and seedling recruitment strongly suggest that recruitment probabilities of wild cherry seedlings are at least partly determined by different seed-dispersal services provided by birds in forest and farmland populations. It is likely that the reduced seed-dispersal distances in farmland populations interact with distance- and density-dependent processes that ultimately determine recruitment success in cherry populations. Future studies that look at processes at the interface between seed dispersal and recruitment success, such as seed predation and pathogen infection, could provide a mechanistic understanding why seedling recruitment is reduced in farmland populations. Such studies should also aim at following recruitment processes from seedling to adult stage (Schupp, Jordano & Gómez 2010).

#### CAVEATS

The combination of movement data from mobile seed dispersers and their gut retention times provide predictions of seed-dispersal distances and the locations of seed deposition (Wang & Smith 2002; Schupp, Jordano & Gómez 2010). Although we predicted seed dispersal by using a simulation approach, we are confident that our predictions reflect seed-dispersal patterns in the real world because our simulations were based on solid empirical data from the study area. Nevertheless, our



modelling approach inevitably included some simplifications of the real-world processes:

1 We used random starting points, restricted to habitats suitable for cherry trees, and therewith assume that blackbirds on average stayed similarly long in fruiting trees and in other woody vegetation.

2 The definition of suitable habitats for wild cherries was based on the ATKIS habitat categories. Therefore, we were unable to resolve potential differences in habitat quality among potentially suitable habitat types.

Furthermore, we only studied a single, albeit very important seed disperser species. Because different dispersers species may deposit seeds differently in the landscape (Jordano *et al.* 2007), future studies should aim at covering a broader spectrum of disperser species, for example, by incorporating both bird and mammal dispersers (Breitbach *et al.* 2012). Similarly, our study investigated a single large-fruited plant species that fruits comparatively early in the year, at a time when most Central European birds are breeding (Bauer, Bezzel & Fiedler 2005). Seed-dispersal patterns could be different in plant species with smaller fruits and later fruiting periods, for instance, *Sambucus* spp. and *Crataegus* spp.

## Conclusions

Our models demonstrate that blackbirds are highly efficient seed dispersers in temperate human-modified landscapes. Blackbirds deposited almost all wild cherry seeds into habitat that is potentially suitable for seedling recruitment, almost independent of the prevailing habitat matrix. We further found that birds can provide seed dispersal over long distances and thus are valuable seed dispersers for plant species with patchy populations in human-modified landscapes. Due to changes in movement behaviour, blackbirds were predicted to disperse wild cherry seeds in the farmland over shorter distances than in the forest. This change in seed-dispersal service was consistent with reduced seedling recruitment in wild cherry populations in the farmland. We conclude that changes in the behaviour of animal seed dispersers can translate into differences in plant population dynamics. In the long term, this may increase the extinction risk of wild cherry populations in farmland.

## Acknowledgements

Feeding trials were supported by Mathias Templin. For radio tracking field-work, we thank Eva Neitscher, Michaela Hanauer, Stefan Ferger, Anne Kotulla, Jonathan Debler, Victoria Miczajka, Florian von Bechtolsheim, Annette Wagner and Jenny Wertheimer. Field studies of seedling recruitment were conducted by Christoph Böhm, Sara Kuntz, Sebastian Menke, Verena Reinhardt and Kathrin Rotter; Wolfgang Wilcke and Yvonne Oelmann provided lab space and supported analyses of soil samples. We heartily thank Jan-Dieter Ludwigs and Benedikt Gießing for their help and the many suggestions concerning the telemetry and the attachment of radio tags. We further thank the Landesuntersuchungsamt Rheinland-Pfalz (LUA) in Koblenz for their permission to work in Rhineland-Palatinate (research permit no. 177-07/G08-1-001) and the Vogelwarte Radolfzell for the ringing permission. Financial support came from the Deutsche Forschungsgemeinschaft (BO 1221/13-1), the Ministry for Environment and Forestry Rhineland-Palatinate and by the research funding programme 'LOEWE – Landes-Offensive zur Entwicklung Wissenschaftlich-

ökonomischer Exzellenz' of Hesse's Ministry of Higher Education, Research, and the Arts.

## References

- Ambos, R. & Kandler, O. (1987) Einführung in die Naturlandschaft. *Mainzer naturwissenschaftliches Archiv*, **25**, 1–28.
- ATKIS Basis-DLM (2011). Landesamt für Vermessung und Geobasisinformation Rheinland-Pfalz, Koblenz, Germany.
- Bauer, H.G., Bezzel, E. & Fiedler, W. (2005) *Das Kompendium der Vögel Mitteleuropas*. 2. Auflage, Aula, Wiesbaden.
- Berens, D.G., Farwig, N., Schaab, G. & Böhning-Gaese, K. (2008) Exotic guavas are foci of forest regeneration in Kenyan farmland. *Biotropica*, **40**, 104–112.
- Böhm, C. (2009) Der Einfluss von Umweltvariablen auf die Rekrutierung und Etablierung von *Prunus avium* L. im Wald- und Feldhabitat in Rheinhessen. Staatsexamensarbeit, University of Mainz, Germany.
- Breitbach, N., Laube, I., Steffan-Dewenter, I. & Böhning-Gaese, K. (2010) Bird diversity and seed dispersal along a human land-use gradient: high seed removal in structurally simple farmland. *Oecologia*, **162**, 965–976.
- Breitbach, N., Tillmann, S., Schleuning, M., Grünewald, C., Laube, I., Steffan-Dewenter, I. & Böhning-Gaese, K. (2012) Influence of habitat complexity and landscape configuration on pollination and seed-dispersal interactions of wild cherry trees. *Oecologia*, **168**, 425–437.
- Cain, M.L., Milligan, B.G. & Strand, A.E. (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany*, **87**, 1217–1227.
- Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519. R package version (adehabitatHR) 0.0-13.
- Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations*. (eds P.J. denBoer & G.R. Gradwell), pp. 298–310. Centre for Agricultural Publishing and Documentations (PUDOC), Wageningen, The Netherlands.
- Da Silva, J.M.C., Uhl, C. & Murray, G. (1996) Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conservation Biology*, **10**, 491–503.
- Dunford, W. & Freemark, K. (2004) Matrix matters: effects of surrounding land uses on forest birds near Ottawa, Canada. *Landscape Ecology*, **20**, 497–511.
- Eshiamwata, G.E., Berens, D.G., Bleher, B., Dean, W.R.J. & Böhning-Gaese, K. (2006) Bird assemblages in isolated *Ficus* trees in Kenyan farmland. *Journal of Tropical Ecology*, **22**, 723–726.
- Fernandez, R., Santi, F. & Doufour, J. (1996) Ausgewähltes Vermehrungsgut der Vogelkirsche in Frankreich. *AFZ/Der Wald*, **51**, 290–294.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R. *et al.* (2005) Global consequences of land use. *Science*, **309**, 570–574.
- Franzén, M. & Nilsson, S.G. (2010) Both population size and patch quality affect local extinctions and colonizations. *Proceedings of the Royal Society of London B*, **277**, 79–85.
- García, D. & Chacoff, N.P. (2007) Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory and seed predation. *Conservation Biology*, **21**, 400–411.
- García, D., Zamora, R. & Amico, G.C. (2010) Birds as suppliers of seed dispersal in temperate ecosystems: conservation guidelines from real-world landscapes. *Conservation Biology*, **24**, 1070–1079.
- Gómez, J.M. (2003) Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography*, **26**, 573–584.
- Graham, C.H. (2001) Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in southern Mexico. *Conservation Biology*, **15**, 1789–1798.
- Grünewald, C., Breitbach, N. & Böhning-Gaese, K. (2010) Tree visitation and seed dispersal of wild cherries by terrestrial mammals along a human land-use gradient. *Basic and Applied Ecology*, **11**, 532–541.
- Haffer, J. (1988) Handbuch der Vögel Mitteleuropas. Band 11/II. Passeriformes (2. Teil): Turdidae. *Echte Drosseln: Turdidae* (ed. U.N. Glutz von Blotzheim), pp. 838–928. Aula-Verlag, Wiesbaden, Germany.
- Hanauer, M. (2010) Zusammenhang zwischen der Streifgebietsgröße von Amseln (*Turdus merula*) und der Intensität der menschlichen Landnutzung. Staatsexamensarbeit, University of Mainz, Germany.
- 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**, 149–158.
- Holbrook, K.M. (2011) Home range and movement patterns of toucans: implications for seed dispersal. *Biotropica*, **43**, 357–364.

- Holbrook, K.M. & Smith, T.B. (2000) Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia*, **125**, 249–257.
- Howe, H.F. & Miriti, M.N. (2004) When seed dispersal matters. *BioScience*, **54**, 651–660.
- Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201–228.
- Janzen, D.H. (1970) Herbivores and number of tree species in tropical forests. *American Naturalist*, **104**, 501–528.
- Jordano, P., García, C., Godoy, J.A. & García-Castaño, J.L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3278–3282.
- Jordano, P., Forget, P.-M., Lambert, J.E., Böhning-Gaese, K., Traveset, A. & Wright, S.J. (2011) Frugivores and seed dispersal: mechanisms and consequences for biodiversity of a key ecological interaction. *Biology Letters*, **7**, 321–323.
- Karubian, J., Durães, R., Storey, J.L. & Smith, T.B. (2012) Mating behavior drives seed dispersal by the long-wattled Umbrellabird *Cephalopterus penduliger*. *Biotropica*, **44**, 689–698.
- Kenward, R.E. (2001) *A Manual for Wildlife Radio Tagging*. Academic Press, London, UK.
- Lenz, J., Fiedler, W., Caprano, T., Friedrichs, W., Gaese, B.H., Wikelski, M. & Böhning-Gaese, K. (2011) Seed-dispersal distributions by Trumpeter Hornbills in fragmented landscapes. *Proceedings of the Royal Society of London B*, **278**, 2257–2264. DOI: 10.1098/rspb.2010.2383.
- Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S. & Haddad, N.M. (2005) Effects of landscape corridors on seed dispersal by birds. *Science*, **309**, 146–148.
- Lewin-Koh, N.J. & Bivand, R., with contributions by Pebesma, E.J., Archer, E., Baddeley, A., Bibiko, H.-J., Dray, S., Forrest, D., Friendly, M., Giraudoux, P., Golicher, D., Gómez Rubio, V., Hausmann, P., Hufthammer, K.O., Jagger, T., Luque, S.P., MacQueen, D., Niccolai, A., Short, T., Stabler, B. & Turner, R. (2011) *Maptools: Tools for Reading and Handling Spatial Objects*, R package version 0.8-10.
- Lundberg, J. & Moberg, F. (2003) Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems*, **6**, 87–98.
- McConkey, K.R. & Brockelman, W.Y. (2011) Nonredundancy in the dispersal network of a generalist tropical forest tree. *Ecology*, **92**, 1492–1502.
- Millennium Ecosystem Assessment (MEA) (2005) Chapter 11: biodiversity regulation of ecosystem services. *Ecosystems and Human Well-being: Current State and Trends, Volume 1, Findings of the Condition and Trends Working Group* (eds R. Hassan, R. Scholes & N. Ash), pp. 297–329, Island Press, Washington, DC.
- Morales, J.M. & Carlo, T.A. (2006) The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. *Ecology*, **87**, 1489–1496.
- Naef-Daenzer, B. (2007) An allometric function to fit leg-loop harnesses to terrestrial birds. *Journal of Avian Biology*, **38**, 404–407.
- Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313**, 786–788.
- Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278–285.
- Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsaoar, A. (2008) Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution*, **23**, 638–647.
- Partecke, J., Van't Hof, T. & Gwinner, E. (2004) Differences in the timing of reproduction between urban and forest European blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? *Proceedings of the Royal Society of London B*, **271**, 1995–2001.
- Pejchar, L., Pringle, R.M., Ranganathan, J., Zook, J.R., Duran, G., Oviedo, F. & Daily, G.C. (2008) Birds as agents of seed dispersal in a human-dominated landscape in southern Costa Rica. *Biological Conservation*, **141**, 536–544.
- Pinheiro, D.B., DebRoy, S., Sarkar, D. & the R Core team. (2009) *nlme: Linear and Nonlinear Mixed Effects Models*, R package version 3.1-96.
- R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: <http://www.R-project.org>.
- Rappole, J.H. & Tipton, A.R. (1990) New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology*, **62**, 335–337.
- Schleuning, M., Huamán, V. & Matthies, D. (2009) Experimental assessment of factors limiting seedling recruitment of an Amazonian understory herb. *Biotropica*, **41**, 57–65.
- Schupp, E.W. (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, **107**, 15–29.
- Schupp, E.W., Jordano, P. & Gómez, J.M. (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, **188**, 333–353.
- Schurr, F.M., Steinitz, O. & Nathan, R. (2008) Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. *Journal of Ecology*, **96**, 628–641.
- Snow, B. & Snow, D. (1988) *Birds and Berries. A Study of An Ecological Interaction*. T & A D Limited, London, UK.
- Spiegel, O. & Nathan, R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, **10**, 718–728.
- Sun, C., Ives, A.R., Kraeuter, H.J. & Moermond, T.C. (1997) Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia*, **112**, 94–103.
- Suszka, B., Muller, C. & Bonnet-Massimbert, M. (1996) *Seeds of Forest Broad-Leaves. From Harvest to Sowing*, 1st edn. INRA, Paris, France.
- Tylianakis, J.M., Tscharntke, T. & Lewis, O.T. (2007) Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*, **445**, 202–205.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.
- UNEP (2007) *Global Environment Outlook GEO4: Environment for Development*. United Nations Environmental Programme, Nairobi, Kenya.
- Wang, B.C. & Smith, T.B. (2002) Closing the seed dispersal loop. *Trends in Ecology and Evolution*, **17**, 379–385.
- Wenny, D.G. (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology*, **3**, 51–74.
- Wenny, D.G. & Levey, D.J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 6204–6207.
- Westcott, D.A. & Graham, D.L. (2000) Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia*, **122**, 249–257.
- Westcott, D.A., Bentrupbäumer, J., Bradford, M.G. & McKeown, A. (2005) Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, **146**, 57–67.

Received 17 January 2012; accepted 28 August 2012

Handling Editor: Mark Rees

## Supporting Information

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

**Appendix S1** Distribution of the regurgitation times (RT): (i) figure with RT distribution curve, (ii) goodness of fit of the parametric distributions and (iii) table with the distribution of RT-values for the drawings.

**Appendix S2** Categorization of habitat from ATKIS DLM data of land-use: (i) suitable habitat and (ii) forest and farmland.

**Appendix S3** Individual seed-dispersal distributions of 32 Common Blackbirds.

**Appendix S4** Individual habitat-specific seed-dispersal distributions of 30 Common Blackbirds: (i) figure for nine forest-dwelling blackbirds and (ii) figure for 21 farmland-dwelling blackbirds.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.