Online Text S1

Detailed description of the study system and field methodologies

Study system

We focused on the plant-frugivore assemblage composed of fleshy-fruited trees and frugivorous thrushes (*Turdus* spp.) in the temperate secondary-growth forest of the Cantabrian range (N Spain), a highly heterogeneous habitat resulting from strong anthropogenic impact. Temperate secondary forest is a common, but highly fragmented habitat type in mid-elevation areas of the Cantabrian range [1]. Typically, secondary forest stands cover less than 30% of surface in these areas, and may occur as fringe patches, adjacent to beech (*Fagus sylvatica*) stands. More frequently, they occur as variable-sized fragments (from isolated remnant trees to patches of several hectares) embedded in a historically deforested matrix of stony pastures and heathland (*Erica* spp., *Ulex europaeus*; [2]. These woodland-pasture areas are traditionally used for extensive cattle raising. Secondary forests are dominated by fleshy-fruited trees, mostly Holly (*Ilex aquifolium*), Hawthorn (*Crataegus monogyna*), Yew (*Taxus baccata*), which account for a large proportion of tree cover (ca. 70%, e.g. [3]. Fruits of these species are 10-14 mm diameter, sugar-rich red berries (arillated seed in yew), and contain 1-4 seeds (5-9 mm). All species ripen in autumn (September to November).

The fruits of the above tree species are consumed from trees by birds and, once fallen to the ground, by carnivorous mammals [4]. Among birds, the main frugivore species are thrushes (*Turdus* sp.) of increasing size (see Table S1.1 in Supporting information Appendix S1): Redwing *T.iliacus*, Song Thrush *T. philomelos*, Blackbird *Turdus merula*, Fieldfare *T. pilaris*, Ring-Ouzel *T. torquatus* and Mistle Thrush *T. viscivorus*. Among these species *T. iliacus, T. pilaris* and *T. torquatus* are over-wintering species in north-western Spain, whereas *T. philomelos, T. merula*, and *T. viscivorus* are resident species that receive overwintering migrants [5]. All thrushes are insectivorous birds whose diet turns to almost exclusively frugivore during autumn and winter. They swallow the entire fruits, defecating (and occasionally regurgitating) the intact seeds in their faeces and, thus, acting as legitimate seed dispersers.

Seed dispersal by thrushes has been shown to affect regeneration of fleshy-fruited trees in the Cantabrian secondary forest, by triggering the processes of re-colonization of deforested areas [6], and by driving the patterns of long-term recruitment at different spatial scales [3,7].

Study site and spatio-temporal framework

The study area was located in the Sierra de Peña Mayor (43º 17'N, 5º 30'W, 900 m a.s.l., Asturias Province, Spain), a mountain range covered by woodland pastures where secondary forest are intermingled with meadows, heathland and limestone rocky outcrops. There, in September 2006, we set up a 400 x 440 m rectangular plot in which the amount of forest cover varied from densely covered sectors to areas of scant cover and isolated remnant trees (see Fig. S1). Thus, the plot was chosen to represent a gradient of forest loss and increasing forest subdivision and forest edge [7]. For sampling purposes, the plot was subdivided into 440, 20 x 20 m cells. Based on previous findings [8], we assumed this spatial framework to have appropriate grain and extent sizes to represent the spatial scale at which frugivory and seed dispersal by thrushes operate. Sampling (see below) was carried out from September to February along three consecutive sampling periods: 2007-2008, 2008-2009 and 2009-2010 (hereafter 2007, 2008 and 2009).

Forest cover and fruit abundance measures

In September 2007, we developed a Geographical Information System (GIS, ArcGIS 9.0) based on a recent (2007) 1:5000-scale ortophotomap image of the study plot. The GIS platform incorporated a grid of 440, 20 x 20 m landscape cells, as well as a layer of digitized forest cover (Fig. S1.1). From this GIS we estimated the amount of forest cover (in m^2, and irrespective of tree species identity) in each cell. We assumed that the per-cell values of forest cover measured in 2007 were also applicable to 2008 and 2009, as actual changes in tree canopy cover in the plot were negligible over years (canopy growth was undetectable at this resolution and tree-fall gaps were very scarce and small).

In autumn of each sampling year, we walked carefully all the study plot, identifying and mapping all individual trees (>1.5 m tall or 4 cm trunk basal diameter) of all species. We assigned visually a standing crop to each tree of any fleshy-fruited species, by means of a semi-quantitative Fruiting Abundance Index (FAI; considering six intervals: 0 = without fruits; 1 = 1-10 fruits; 2 = 11-100; 3 = 101-1,000; 4 = 1,001-10,000; 5 $\geq$ 10,001). Fruiting is quite synchronous among individuals and species within the Cantabrian secondary forest, with almost all fruit ripening delimited to 1-2 months (although fruits may remain attached to trees for 1-3 additional months). We thus considered that a sampling of fruit abundance at the beginning of the season provided an appropriate estimate of the spatial template of fruit resources for frugivores through the season. As *T. baccata* show earlier fruiting peaks than the remaining fruiting species, we first walked the plot in late September to survey the crops of these species, and walked again the plot in late October, recording the fruit crops of all remaining fleshy-fruited species. All data on position, species and FAI of each individual tree, every sampling year, were incorporated into the GIS platform. We calculated the total abundance of fruits per cell, and the abundance of fruits of different tree species, per year as the sum of the crops of all fruiting trees present each year. Crops were extrapolated from FAI ranks, taking into account the fit between the actual crop size of a sub-sample of trees and the assigned FAI index, using an allometric equation (*crop size* = 1.77 × exp(1.92 FAI), $R^2 = 0.80$; $N = 136$ trees [9].

Bird feeding activity and movement

Foraging patterns of thrushes were sampled over observation sequences made from five different vantage positions in elevated outcrops (hill tops), located along the central axis of the plot (Fig. S1). Sampling season extended from October to February. Observation time was 78, 90 and 79 h for 2007, 2008 and 2009, respectively. In each sequence, a movement bout of a given individual bird was tracked with the help of 8 x 30 binoculars, a chronometer, and printed maps of plot cells. Once a given focal bird was located, it was followed until lost either because it left the plot or disappeared into the canopy). For all sequential steps in the movement bout (i.e. consecutive rests separated by intervening flights), we recorded the duration and location of the resting site (i.e. the cell within the plot), and the species and number of fleshy fruits eaten while perching in a fruiting tree. Flight distance was calculated for each flight between rests located in different cells as the Euclidean distance between the centroids of the starting point and endpoint cells.

Sampling of seed dispersal by thrushes in the field

Bird-dispersed tree seeds are unequivocally identifiable: they are clean of pulp remains, unlike seeds on fruits fallen beneath trees, and occur in small clusters easily distinguishable from those occurring in mammal faeces, and they can be almost exclusively attributable to thrushes [4]. We assessed the occurrence of seeds dispersed by thrushes in sampling stations across the whole plot in 2009. Ten sampling stations, separated from each other by 2 m, were placed along the central longitudinal axis of 220 sampling cells following a checkered pattern (see Fig. S1). In each station, we set up a permanently labelled, open-ground 50 x 50 cm quadrat where all tree seeds dispersed by birds were collected and counted. Each sampling station was assigned to covered (tree canopy) or open (pasture, rock) microhabitats, corresponding to the structural features of the area covered by (or above) the quadrat. We estimated the number of dispersed seeds per tree species sampling station as the sum of seeds found in two consecutive surveys (late November 2009 and early January 2010). Previous studies in the same site demonstrated that this methodology provides estimates of seed abundance and richness reliable enough for the evaluation of the large-scale patterns of seed dispersal [3,8]. In fact, seed removal by diurnal animals was never observed, and removal by nocturnal rodents is low during most of the dispersal season (predation frequency peaks late in winter, [10]. In any case, those seeds showing signs of predation (open husks or teeth marks) found in the quadrats were considered as dispersed seeds.

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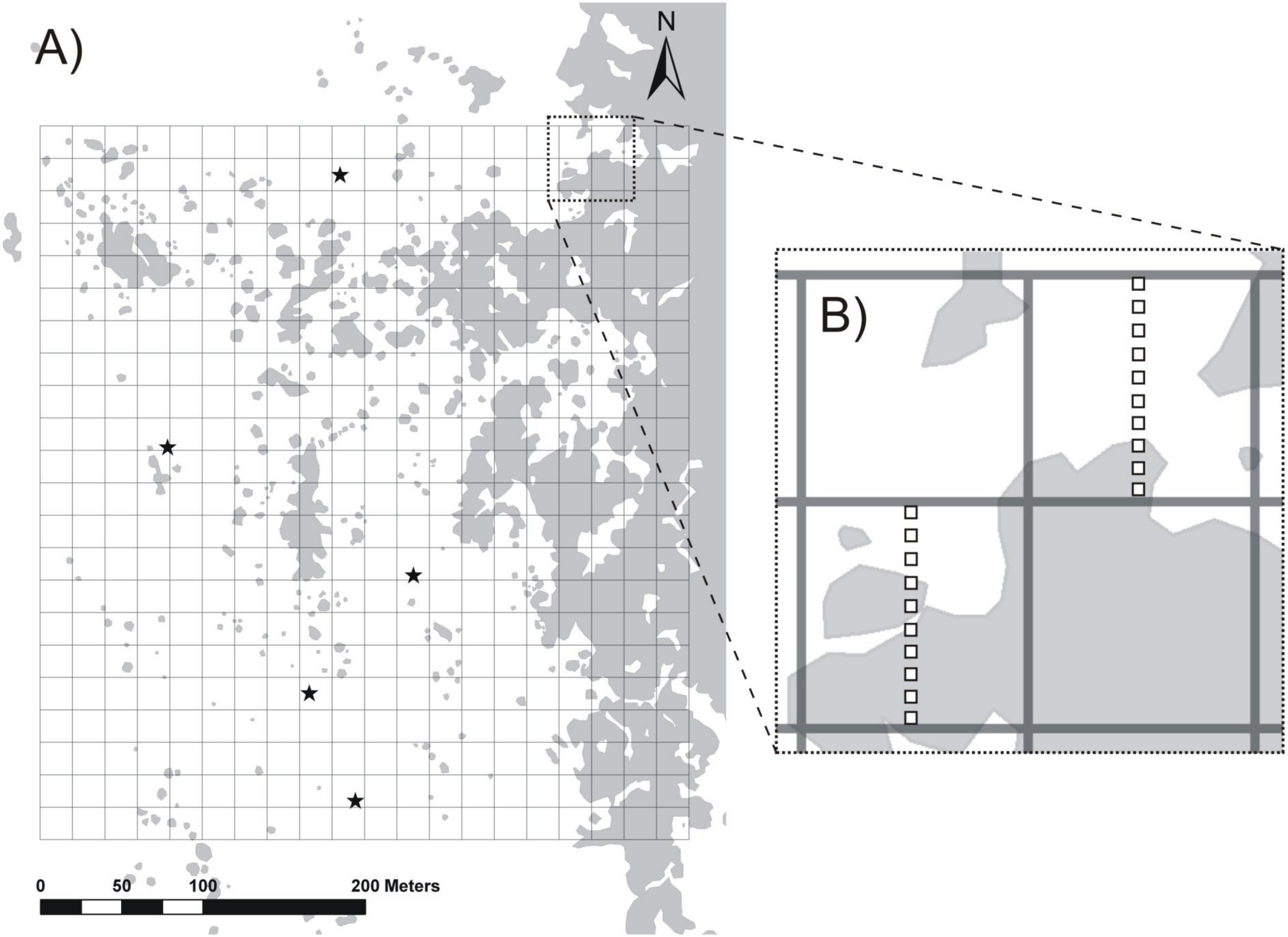
Figure S1.1. Scheme of the field study plot representing: A) the configuration of the forest cover (grey area), the plot subdivision into 20x20 m landscape cells, and the vantage (black stars) positions for bird observation; B) a detail of the position of the stations for sampling seed deposition by frugivores (white squares) along the central longitudinal axis of cells following a checkered-pattern.



Online Text S2

Gut Passage Time estimation for *Turdus* sp. and seeds of fleshy-fruits in the Cantabrian Range

Regurgitation *vs.* defecation

We have calculated Gut Passage Time (GPT) distribution based exclusively on seed defecation times. Although seed regurgitation from fleshy-fruited species, like *Crataegus monogyna* and *Prunus avium*, has been observed (e.g. *Turdus merula* in captivity, Sorensen 1984; Breitbach et al. in press), we assumed that seed regurgitation of fleshy-fruited species by *Turdus* sp. is very rare in the Cantabrian Range, by the following reasons:

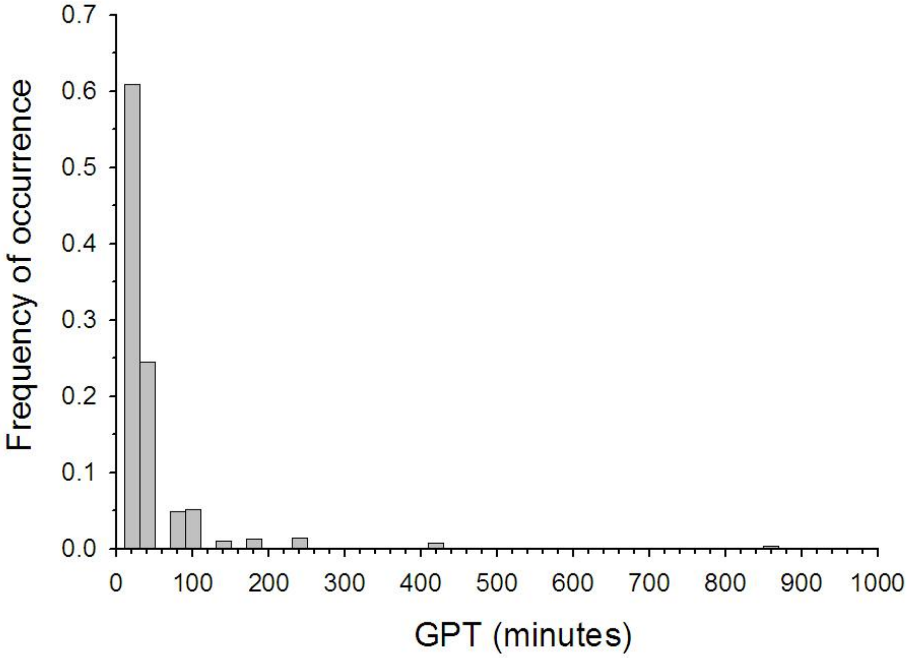
1) Sorensen's finding was probably related to the much larger seed mass of *C. monogyna* fruits used in her study (130 mg in Soresen 1984 vs. 87 mg in García et al. 2005). Similarly, regurgitation of *P. avium* seeds was associated to its big size (fruit diameter > 15 mm), much bigger than those of the fleshy-fruited species studied here.
2) We had never observed regurgitation in the field (from aprox. 450 hours of direct observation on foraging sequences of individual birds of different species across 3 years). Similar results have been found in other studies in the same fruit-frugivore system in northern Spain (Guitián et al. 2002).
3) Regurgitation has been found to be rare (<5% of ingested seeds) in other captivity studies involving thrushes and fleshy fruits in the range of size of the studied here (*Turdus helleri* eating *Xymalos monospora*, Lehouck et al. 2009; *Turdus merula* eating *Crataegus monogyna*, Sobral et al. 2010; *Turdus merula* eating *Myrtus communis*, M. Sobral, A.R. Larrinaga & L. Santamaría unpublished)

GPT values and distribution

As no empirical data on the distribution of values of GPTs was available from any of the studied bird-fruit species pairs, we used data from a similar bird-fruit species pair: *Turdus merula* eating fruits of *Myrtus communis* (Mar Sobral, Asier R. Larrinaga & Luis Santamaría, unpublished data). GPT measures were done in January 2006 at the Institut für Vogelforshung, Vogelwarte Helgoland (Germany). Feeding trials in captivity conditions involved 18 hand-raised and wild *Turdus merula* individuals (see Sobral et al. 2010 for a comprehensive description of aviary conditions and bird care methodology in a similar study). GPT was measured as the time from swallowing to defecation per individual seeds. Average GPT resulted in 39.35 min. (±2.29SE; CV=173.98; N=890 seeds; Fig. S.1.1). This value was only slightly longer than that found by Breitbach et al. (in press) for seed regurgitation of *P. avium* seeds by *T. merula* (median 29.6 min).

Given the similarity of fruits of *Crataegus monogyna*, *Ilex aquifolium* and *Taxus baccata* in the Cantabrian range (in terms of fruit mass; seed load; pulp to seed ratio) we assumed that average values and distribution of frequencies of GPTs were equivalent between tree species for *T. merula*, and similar to that found in *Myrtus communis*. In fact, no relationship between fruit or seed size and GPT across species has been found for *Turdus merula* (Sorensen 1984). We assumed that in *Ilex aquifolium*, all seeds per fruit (average 3.5 seeds/fruit) were defecated at the same time (the average number of seeds per dropping defecated in the field is 3.4; Martínez et al. 2008; see also Guitián et al. 2002).

Figure S2.1. Frequency distribution of gut passage time for *Myrtus communis* seeds defecated by *Turdus merula*.



Extrapolation from *Turdus merula* to other *Turdus* spp. Relationship between bird body size and GPT:

We calculated a body size-GPT relationship from Herrera (1984) using 8 species from Turdidae and Silvidae, and the GPT of a Barium Sulfate solution:

GPT = 23.73 + 0.51*weight
Slope: 0.511±0.14
Linear regression $R^2 = 0.68$; $F_{1,6} = 12.74$; P = 0.012

Using the slope of this relationship, we calculated an intercept of -11.76 corresponding to a GPT of 39.35 min (which is the average GPT value for *Myrtus communis* seeds for *Turdus merula* in captivity, Fig. 1). Thus, the relationship between the *Turdus* body size and GPT for any fleshy-fruit species should be based on the relationship

$$\text{GPT} = -11.76 + 0.511*\text{weight} \qquad (0.1)$$

Thus, to extrapolate GPT for species other than *Turdus merula*, we used GPT distribution of *Myrtus communis* in *Turdus merula* and transform GPT data by using the proportions between species obtained from GPT in eq. (0.1) given the coefficients from Table 1. For example, a GPT=15 min in *Turdus merula* would correspond to 8.17 (=15*0.545) min in *Turdus iliacus*, 16.93 min in *Turdus pilaris*, 10.15 min in *Turdus philomelos*, etc.

Table S2.1. Coefficients of GPT for different species of thrushes based on body size and refereed to *Turdus merula* GPT.

Species	Body size (g)*	mean GPT estimate	Rate for Gamma distribution†
T. iliacus	65	21.45	0.074
T. pilaris	110	44.45	0.0357
T. merula	100	39.34	0.04
T. philomelos	75	26.57	0.0598
T. torquatus	120	49.56	0.032
T. viscivorus	130	54.67	0.029

* from Collar (2005)

† assuming the shape parameter is 1.59 as in the Gamma distribution fitted to the data from *Turdus merula* above.

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Online Text S3

Analysis for perching time and fruit consumption for the six *Turdus* species followed in the field.

Figure S3.1. Observed and fitted distributions of time perching for the six *Turdus* species.

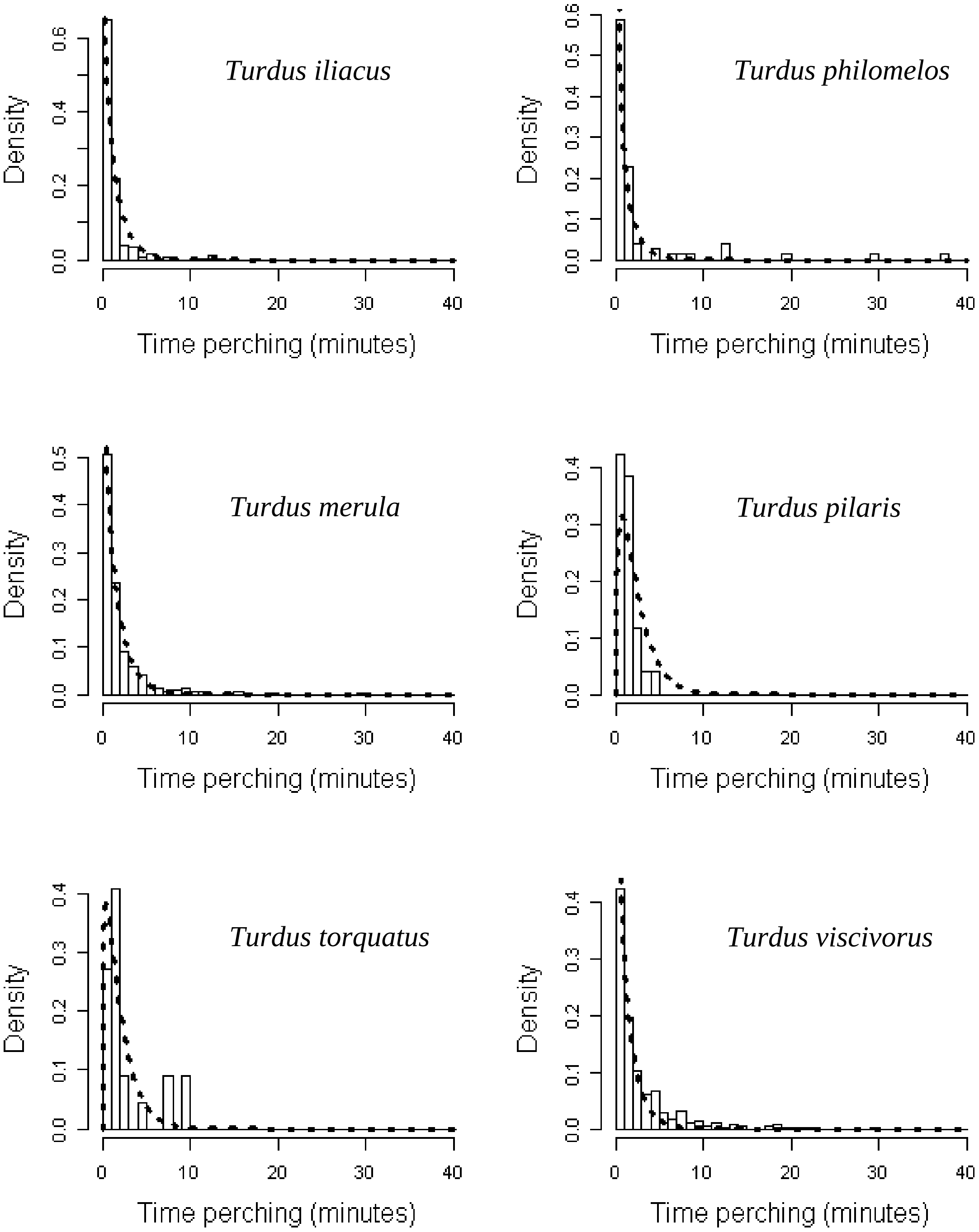


Table S3.1. Parameters with SE in parenthesis for Gamma distributions of time perching at plants or standing on the ground

	shape	rate	Expected (min)	Median (min)	N
Turdus iliacus	0.849 (0.067)	0.638 (0.067)	1.331	0.633	244
Turdus philomelos	0.569 (0.077)	0.204 (0.042)	2.796	0.833	75
Turdus merula	0.931 (0.054)	0.492 (0.037)	1.891	1.000	458
Turdus pilaris	1.472 (0.371)	1.114 (0.334)	1.322	1.166	26
Turdus torquatus	1.256 (0.339)	0.435 (0.144)	2.883	1.708	22
Turdus viscivorus	0.747 (0.044)	0.269 (0.022)	2.773	1.416	427

Table S3.2. Pearson's product-moment correlations between perching time and fruit consumption for all species

	r	t and df	p - value	CI
Turdus iliacus	0.131	t = 1.743, df = 175	0.0831	-0.017 0.273
Turdus merula	-0.009	t = -0.1648, df = 284	0.8692	-0.126 0.106
Turdus philomelos	0.200	t = 1.4582, df = 51	0.1509	-0.074 0.446
Turdus pilatus	0.369	t = 1.5894, df = 16	0.1315	-0.118 0.713
Turdus torquatus	-0.224	t = -0.6899, df = 9	0.5077	-0.726 0.434
Turdus viscivorus	0.076	t = 0.9586, df = 158	0.3392	-0.080 0.229

Table S3.3. Zero –inflated Poisson model for fruit consumption. For each species we estimated the probability of consuming fruits and the mean of a Poisson distribution (Lambda). Confidence intervals based on profile Likelihoods are reported in parenthesis.

	Probability of fruit consumption	Average number of fruits per feeding bout	N
Turdus iliacus	0.531 (0.458 – 0.603)	5.168 (4.725 – 5.639)	179
Turdus philomelos	0.370 (0.249 – 0.503)	6.560 (5.530 – 7.791)	54
Turdus merula	0.524 (0.467 – 0.580)	5.916 (5.541 – 6.307)	296
Turdus pilaris	0.500 (0.281 – 0.719)	6.556 (5.022 – 8.373)	18
Turdus torquatus	0.455 (0.194 – 0.735)	5.560 (3.773 – 7.937)	11
Turdus viscivorus	0.335 (0.266 – 0.409)	5.145 (4.569 – 5.768)	164

Online Text S4

Model fit, comparison and assessment for movement rules of *Turdus* species in the study plot

Table S4.1

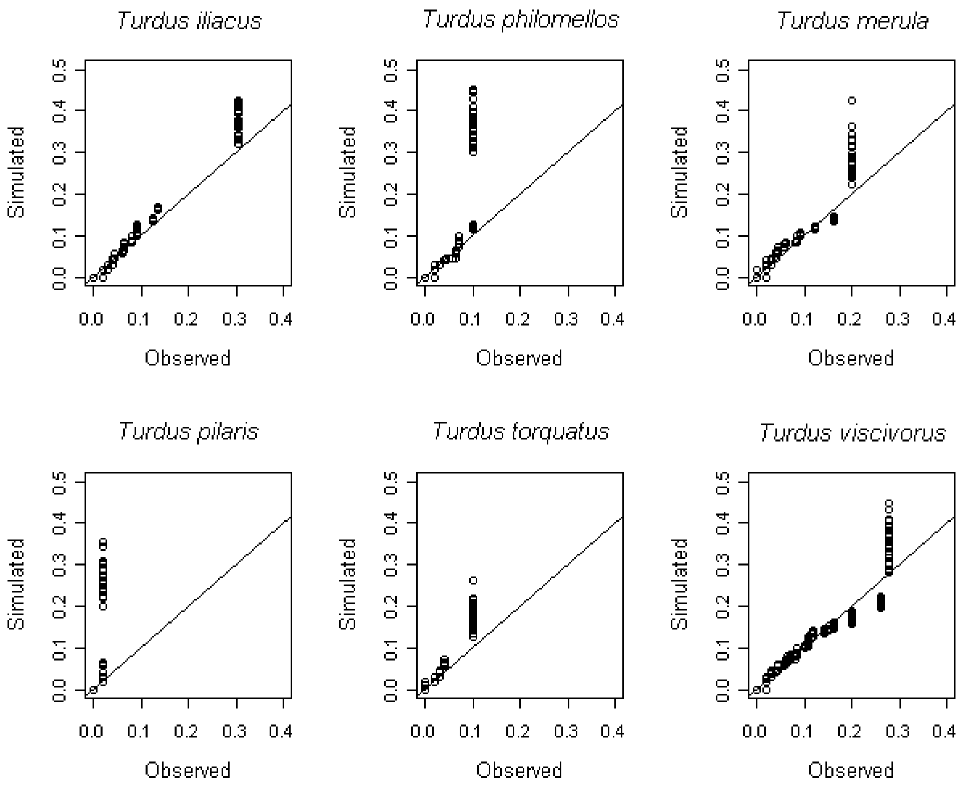
Parameter values and standard errors for the movement models (equations 1 and 2 in the main text) of the six *Turdus* species followed in the field.

	T. iliacus	*T. philomelos*	*T. merula*	*T.pilaris*	*T. torquatus*	*T. viscivorus*
a_d	-4.407 (0.135)	-3.717 (0.228)	-4.093 (0.079)	-3.669 (0.400)	-3.662 (0.434)	-3.905 (0.107)
b_d	-0.647 (0.0608)	-0.398 (0.114)	-0.437 (0.046)	-0.406 (0.212)	-0.242 (0.293)	-0.517 (0.050)
a_c	1.082 (0.798)	0.746 (0.372)	0.252 (0.025)	0.269 (0.134)		0.192 (0.049)
b_c	1.397 (0.304)	1.762 (0.469)	3.278 (0.634)	2.382 (1.457)		1.477 (0.547)
a_f	16.833 (100.907)	3.577 (16.023)	2.582 (6.762)		0.105 (0.003)	0.0978 (0.018)
b_f	0.601 (0.155)	0.847 (0.265)	0.335 (0.114)		50.119 (28.732)	2.198 (4.194)
a_o	-0.073 (0.523)	-1.429 (0.842)	-1.078 (0.382)	0.361 (1.503)	0.714 (1.739)	-0.698 (0.2689)
b_o	-3.718 (0.901)	-1.361 (0.991)	-1.752 (0.438)	-3.527 (2.732)	-2.643 (2.303)	-0.885 (0.291)

Table S4.2 Delta AICc for all models and species

	T. iliacus	*T. merula*	*T. viscivorus*	*T. philomelos*	*T. pilaris*	*T. torquatus*
distance, cover and fruit	0	1.7	0	0	8.8	11.4
distance and cover	5.7	0	29.8	2.2	0	4.1
distance and fruit	56.1	103.4	29.8	22.2	4.6	0
distance only	121.4	166.4	25.7	62.2	3.5	2.5

Figure S4.1. quantile-quantile plots of distance moved for observed and simulated thrushes.


Turdus iliacus

Turdus philomellos

Turdus merula

Turdus pilaris

Turdus torquatus

Turdus viscivorus

Online Text S5

Assessment of landscape-scale spatial structure of observed and predicted seed rain.

Spatial aggregation of the seed rain

We characterized the landscape-scale spatial structure of predicted and observed seed rain of the different tree species (*Crataegus monogyna*, *Ilex aquifolium* and *Taxus baccata*) by quantifying the degree of spatial aggregation (patchiness) in the abundance of dispersed seeds. For that, we used the Spatial Analysis by Distance Indices (SADIE; Perry 1995; Perry et al. 1999), a method that describes the spatial structure of ecological data sampled in the form of spatially geo-referenced counts, identifying and locating the areas where patches of high- or low density occur.

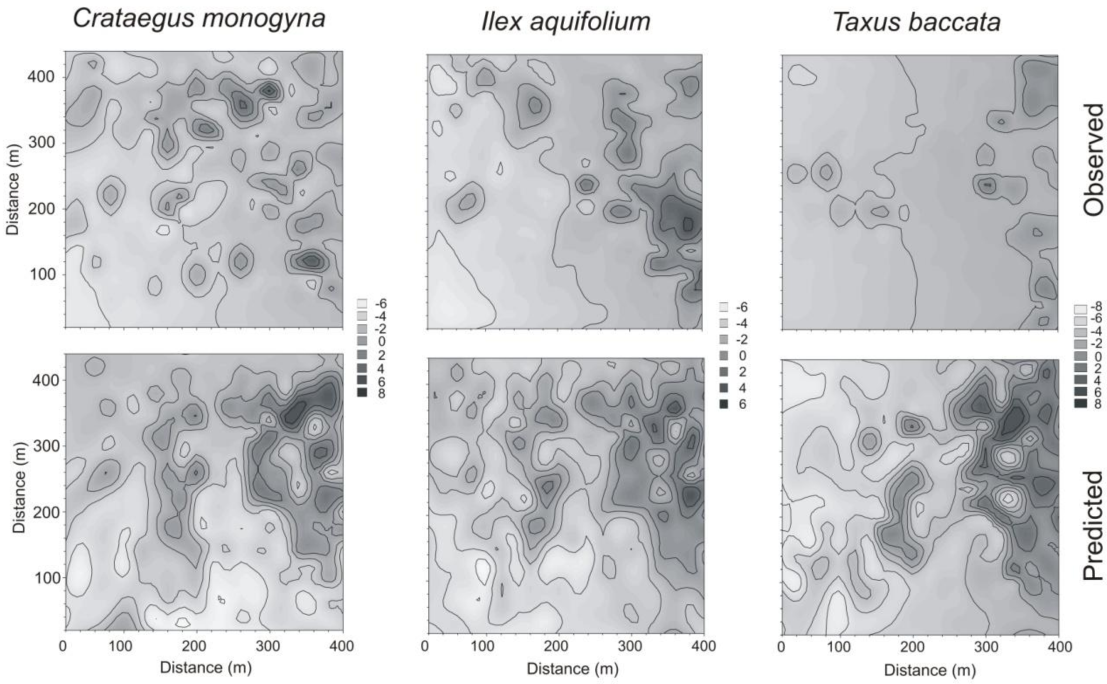
We estimated, for the cell subset of field sampling (N=220), the abundance of dispersed seeds per cell observed in the field (from the average number of seeds per sampling station), and the corresponding abundance predicted by the model, for each tree species. Seed counts were referenced in space by the x,y coordinates of cell centroids. Based on estimates of distance to regularity (i.e. the difference between the true count value in a given point and a count value assuming a regular distribution of all counts across sampling points), SADIE provides an aggregation index (*Ia*) to measure the degree of overall spatial clumpiness across the whole plot extent, representing random (*Ia* = 1), regular (*Ia* < 1) or aggregated (*Ia* > 1) distribution patterns. The degree of significance of *Ia* is checked by means of a randomization procedure based on rearrangements of the observed counts amongst the sample units. SADIE also provides a point-level parameter, the clustering index (υ), which quantifies the degree to which the count at a given point contributes to the overall clumpiness. Points with high positive υ values contain big counts which contribute greatly to the generation of high-density clusters (“patches”), whereas points with negative υ values contain small counts which contribute to low-density clusters (“gaps”; e.g. Figure S5.1).

The aggregation indexes of both observed and predicted abundances of dispersed seeds at the landscape scale indicated strong and significant patchiness, with higher values on predicted seed rain than of observed seed rain, for all species (Table S5.1). Aggregation was stronger on *I. aquifolium* seed rain than on those of *C. monogyna* and *T. baccata*, in both the observed and predicted estimates.

Table S5.1. Indexes of aggregation (*Ia*) quantifying the degree of non-random patchiness in the seed rain of different tree species, both that observed in the field (average number of seeds per m2 per cell, 2009 data; n=220 cells) and that predicted by the model (number of seeds per cell, 2009 data; n=220 cells), with their associated significance degree (***: P < 0.001).

Species	Observed seed rain	Predicted seed rain
Crataegus monogyna	1.83 ***	2.42 ***
Ilex aquifolium	3.62 ***	3.93 ***
Taxus baccata	1.96 ***	3.68 ***

Figure S5.1. Distribution of the abundance of dispersed seeds of different tree species across the study plot. Grey-scaled lined contours represent the SADIE-provided clustering indexes (υ) for of observed and predicted seed rain. Note the different scales between species.



Spatial match between observed and predicted seed rain

We also used SADIE to estimate the match between the spatial distributions of observed and predicted seed rains, in order to assess the ability of model-inferred seed rain to predict the large-scale spatial structure of seed dispersal in the field. For that, we related the clustering vectors of the observed seed rain with those of the seed rain predicted by the model in the same cells. Analyses relating clustering vectors must account for the potential effects of spatial autocorrelation in the determination of correlation strength. In this sense, the association index $X_{p,}$ (Perry & Dixon 2002) quantifies the degree of spatial association/dissociation between two variables sampled at the same points. This index ranges between + 1 (complete spatial association) and -1 (complete dissociation), with 0 indicating spatial independence. The statistical significance of X_p is quantified by the Dutilleul method, which corrects the amount of degrees of freedom in the presence of spatial autocorrelation. Complementarily, in order to estimate the proportion of the variance in the patchiness of the observed seed rain explained by that predicted by the model, we regressed the clustering indexes of observed (response) and predicted (predictor) seed rain by means of Spatial Simultaneous Autoregressive Models (SAR, Keitt et al. 2002).

The seed rain predicted by our mechanistic model reproduced quite well the landscape scale spatial structure of observed seed rain. For all study tree species, there was a positive and significant spatial match between the landscape-scale patchiness of observed seed rain and that of seed rain predicted by the model, increasing from *C. monogyna* to *I. aquifolium* and *T. baccata* (Fig. 1; Table S5.2). In the last species, predicted seed rain accounted for 45% of the variance of observed seed rain.

Table S5.2. Spatial match between observed and predicted seed rains. The indexes of association (*Xp*), measuring the correlation between clustering indexes of observed and predicted abundance of dispersed seeds (n=220 cells), and their corresponding significance levels (corrected by Dutilleul's method) are shown. Results of SAR considering the clustering indexes of observed seed rain as a response variable and those of predicted seed rain as predictor are also shown (R^2 indicates the proportion of variance explained by predictor, without space effect).

Species	*Xp*	Corrected N	P	R^2*	t-value	P
Crataegus monogyna	0.356	198.8	<0.001	0. 119	4.56	<0.001
Ilex aquifolium	0.596	173.8	<0.001	0.324	8.37	<0.001
Taxus baccata	0.695	189.5	<0.001	0.452	10.25	<0.001

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