

1 **Large-scale features affect spatial variation in seed dispersal by birds in juniper**  
2 **woodlands**

3 **José L. Tellería · Luis M. Carrascal · Tomás Santos**

4

5 Concise title: Seed dispersal by birds

6

7 J. L. Tellería · T. Santos

8 Dept. de Zoología y Antropología Física, Universidad Complutense, CEI-Moncloa, 28040

9 Madrid, Spain.

10

11 L. M. Carrascal

12 Dept. Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, MNCN-CSIC, E-

13 28006 Madrid, Spain

14

15 \* Corresponding author: José L. Tellería.

16 E-mail: [telleria@bio.ucm.es](mailto:telleria@bio.ucm.es)

17 Telephone: + 34 91 394 4943

18 Fax: +34 91 394 4947

19

20

21 **Abstract** Fruit-frugivore interactions have received great attention from evolutionary,  
22 ecological and applied perspectives. However, despite the fact that large-scale approaches may  
23 offer new insights on fruit-frugivore interactions, little work has been devoted to explore the  
24 factors shaping large-scale variation of seed dispersal. This paper studies the spatial variation in  
25 seeds regurgitated within pellets by wintering thrushes (*G. Turdus*) in a set of 26 Spanish  
26 juniper (*Juniperus thurifera*) woodlands scattered along a latitudinal gradient during two  
27 winters of contrasting cone and bird abundance. It explicitly explores whether pellet rain  
28 variation among woodlands was related to changes in vegetation cover, temperature, day length  
29 duration and bird abundance. Top regression models in the AIC framework explained 34% and  
30 70 % of variance in pellet numbers in low and high crop and bird abundance years, respectively.  
31 In both winters, the spatial variation in pellets correlated to thrush abundance and day length  
32 variation. Pellet abundance linked to cone distribution only in the year of high crop, in which  
33 many migratory, extra-Iberian thrushes arrived to exploit the resource. Strong dependence of  
34 seed dispersion on large-scale features affecting bird numbers (e.g. the arrival of extra-Iberian  
35 migratory birds) and feeding behaviour (e.g. latitudinal variation in day length duration)  
36 suggests a primary role for variables acting at large scales on this mutualistic interaction.

37

38 **Key-words** Frugivorous birds · *Juniperus thurifera* · large-scale fruit tracking · pellet rain ·  
39 seed dispersal · *Turdus* sp.

40

## 41 **Introduction**

42 Fruit production is a common evolutionary strategy developed by plants to improve seed  
43 dispersal by frugivorous animals. Because it affects the fitness of individual plants, fruit-  
44 frugivore interactions have received great attention from evolutionary, ecological and applied  
45 perspectives (Levey et al. 2002; Schupp et al. 2010). However, little work has been explicitly  
46 devoted to explore the features affecting the geographical distribution of seed dispersal despite

47 large-scale approaches may offer new insights on fruit-frugivore interactions (Kollmann 2000;  
48 Herrera 2002; García et al. 2011).

49         Seed dispersal depends on the abundance of fruit-producing plants, the number of  
50 dispersers and their ability to move the seeds (Schupp 1993). In this process, birds are of  
51 paramount importance, since they fly over large areas in the search of fruit food (Levey and  
52 Stiles 1992). When they find a suitable patch, they spend a substantial proportion of time on the  
53 fruiting plants producing a rain of seeds within pellets, faeces or fruit remains. In this way, birds  
54 establish a dynamic link between the fruiting plants and numerous microhabitats, habitat  
55 patches or other targets for seed dispersion. In addition, widespread dispersal of pellets  
56 increases the chance of occupying suitable places for seedlings, a process that improves local  
57 recruitment and reinforces the persistence of populations (Wenny 2001). This is a “context  
58 sensitive” process dependent on the conditions of each study site (Jordano 2000) that will rely  
59 on the ability of seed dispersing birds to track the patterning of fruit availability at different  
60 spatial and temporal scales (Schupp et al. 2010).

61         This paper studies the spatial variation in pellets produced by wintering thrushes (*G.*  
62 *Turdus*) in 26 woodlands distributed in a large area within the Iberian range of the Spanish  
63 juniper (*Juniperus thurifera*; Fig.1). Pellet abundance within a woodland may be considered as  
64 an index of seed dispersion activity by these birds, which are reputed as the main dispersers of  
65 juniper seeds in the Mediterranean (Jordano 1993, Santos et al. 1999, Escribano-Ávila 2012).  
66 More explicitly, the paper tries to show if pellet distribution follows cone abundance among  
67 woodlands or is distorted by some features affecting seed dispersing thrushes. It may be  
68 assumed that the variation of pellet abundance will rely, in the first place, on the ability of  
69 thrushes to match the spatio-temporal distribution of this resource each winter (Tellería et al.  
70 2008, 2013). But seed-dispersing birds may fail to track cone abundance if they are unable to  
71 perceive food availability in the whole exploited region (Kotliar and Wiens 1990; García and  
72 Ortiz-Pulido 2004; García et al. 2011), avoid some areas in spite of cone abundance (e.g., colder  
73 sectors; Root 1988), or have difficulties in allocating individuals among woodlands according to  
74 food availability when regional populations are small (Fretwell 1972; Gaston et al. 2000). If

75 thrushes fail to track cone abundance, they will not remove seeds according to the actual crops  
76 of the juniper woodlands. This will produce an uneven contribution of these birds to seed  
77 dispersal effectiveness among populations (Myers and Harms 2009; Schupp et al. 2010).

78 To address these questions, we explored interactions between pellet distribution and the  
79 abundance of thrushes and ripe cones in the 26 study woodlands during two winters of  
80 contrasting cone and bird abundance (2009-2010 and 2010-2011). In addition, we controlled the  
81 effect of three additional features that might distort the ability of birds to deliver pellets  
82 according to cone abundance distribution. First, vegetation structure may influence thrush  
83 distribution and the abundance of perching sites, two features affecting seed rain (Hutto 1985;  
84 Holl 1998; Alcántara et al. 2000; Jordano and Gody 2002; Herrera and García 2010). Second,  
85 low temperatures will raise the energy demanded by birds in colder woodlands forcing thrushes  
86 to increase food intake and pellet production (e.g. Calder and King 1974; Kwit et al. 2004).  
87 Finally, since pellet production (the ingestion of ripe cones and the rapid elimination of non-  
88 nutritional seed “ballast”; Sorensen 1984) is a time-consuming process, longer days in southern  
89 woodlands will increase the time available for foraging and producing pellets (Carrascal et al.  
90 2012).

91

## 92 **Methods**

93 The juniper-thrush system

94 Spanish juniper woodlands are the wintering grounds of many thrushes (*Turdus iliacus*, *T.*  
95 *pilaris*, *T. viscivorus*, *T. philomelos*, *T. merula*, *T. torquatus*), most of which move to Spain  
96 from central and northern Europe (Santos 1982; Santos et al. 1983). This juniper shows a  
97 complex pattern of cone production, with sharp inter-winter and inter-site changes in crop size  
98 (Montesinos 2007) that thrushes track across extensive areas (Jordano 1993). These birds  
99 regurgitate pellets, which are cylinders *ca.* 1 cm long and 3 mm wide comprised of fruit fibres  
100 and 2-3 seeds, inside and around the focal feeding places, including vegetation patches without  
101 cones (Santos et al. 1999; Tellería et al. 2011). Although other animals (deer, sheep, carnivorous  
102 mammals, rabbits, etc.) disperse juniper seeds, thrushes appear to be the most effective and

103 ubiquitous dispersers of this tree within these woodlands (Santos et al. 1999; Escribano-Avila et  
104 al. 2011).

105

#### 106 Study area

107 The study was carried out in 26 localities encompassing the main range of the Spanish juniper  
108 in the Iberian Peninsula (Fig. 1). The altitude of the study localities ranged between 950  
109 and 1314 m a.s.l.. This juniper forms open woodlands where dominant junipers mix with  
110 isolated patches of other species (*Quercus ilex*, *Q. faginea*, *Pinus spp.*). They extend over  
111 125,000 hectares, mostly between 800-1200 m.a.s.l., in areas dominated by hot summers and  
112 cold winters with annual precipitation of 400-500 mm. Winter conditions are severe, with low  
113 average temperatures (mean values between 1.8°C and 4°C), freezing period from mid-October  
114 to late-May, and relatively frequent snowfalls (average of ten days per year; Ninyerola et al.  
115 2005). The weather during the two study winters (December to 15<sup>th</sup> February, 2009-2010) was  
116 characterized by frequent snowfalls (19% of the days) and low average minimum temperatures  
117 (-1.2 °C). Snowfalls were associated with cold spells that affected the whole sample of  
118 study localities in a similar fashion. A large proportion of days showed minimum  
119 temperatures below 0°C (56% of the days; data from Instituto Nacional de Meteorología  
120 averaged for Burgos -859 m.a.s.l.- and Teruel -915 m.a.s.l., meteorological stations, located at  
121 both latitudinal limits of the study region).

122

#### 123 Bird and cone abundance

124 Thrushes were counted along 0.5-km line transects located at the study woodlands in winters  
125 2009-2010 and 2010-2011. We counted all the individuals without distinction of distance to the  
126 line transect to collect more records and, in this way, to have a more comprehensive assessment  
127 of local abundances. The counts were repeated in December, January and February to  
128 encompass the main wintering period of migratory thrushes. The location of line transects was  
129 recorded using a portable GPS receiver. From these three counts per winter, we obtained the

130 mean number of thrushes detected per transect, as an index of the relative abundance in each  
131 locality. Abundance of ripe cones in both study winters was assessed in 20 Spanish junipers  
132 spaced 25 m alongside every line transect used to count birds. The selected trees were marked  
133 with numbered labels and recoded with GPS devices for easy subsequent detection. In these  
134 randomly selected junipers we counted by eye, after training, the number of ripe cones, which  
135 are those selected by thrushes (Tellería et al. 2011). Ripe cones were distinguished considering  
136 colour and size (blue or blue-black, succulent and sweet to taste). We counted cone availability  
137 each winter in the last week of November just at the start of the wintering period of thrushes.

138

139 Pellet abundance and vegetation structure

140 We looked for pellets under the canopy of 10 junipers used to assess cone abundance at each  
141 study site (regularly spaced 50 m alongside every line transect). We repeated the counts three  
142 times each winter on the same day that bird abundance was assessed. In each counting session,  
143 we removed all pellets under the canopy to prevent its repeated sampling. We used the average  
144 of the cumulative number of pellets recorded under each sampling tree as the pellet rain in the  
145 26 study localities. Structure of the arboreal layer was recorded in a 500 x 10 m belt (5000 m<sup>2</sup>)  
146 over the 26 line transects. Tree density was estimated by counting the number of Spanish  
147 junipers and other tree species > 2.5 m height. The Spanish juniper was the dominant tree (95%  
148 of trees recorded), with pines (*Pinus spp.*), Holm oaks (*Quercus ilex*) and some deciduous oaks  
149 (*Q. faginea*) as other scarce species in the studied woodlands. We also measured the diameter of  
150 the canopy of each juniper to control for the effect of the area under which we counted the  
151 pellets. Nevertheless, after exploring the data, we discarded the inclusion of tree crown diameter  
152 in our analyses, as average number of pellets and juniper diameter were uncorrelated  
153 (Spearman's rank correlation coefficient in 2009:  $r=0.045$ ,  $P=0.826$ ; in 2010:  $r=0.157$ ,  $P=0.443$ ;  
154  $N=26$  in both winters).

155

156 Air temperature and day length duration

157 Winter air temperature was assessed at each study site with one temperature logger (HOBO  
158 Pendant<sup>®</sup> Temperature/Light Data Logger 64K, Cape Cod, Cape Cod, Massachusetts ) located  
159 at the centre of each line transect. Data loggers were placed on thick juniper trunks covered by a  
160 dense layer of branches, oriented to the north at approximately 1.5 m above ground, and  
161 recorded air temperature every ten minutes from 1<sup>st</sup> December to 15<sup>th</sup> February of winters 2009-  
162 2010 and 2010-2011. For each recording day (144 measurements) we obtained the average  
163 temperature, maximum daytime temperature and the minimum night temperature. For each  
164 study woodland, we averaged temperatures for the 77-day study period. These three temperature  
165 measurements were highly correlated across woodlands ( $r > 0.8$  in all cases). Thus, we selected  
166 the average minimum night temperature considering its clear functional meaning related to  
167 maximum thermoregulatory costs at night, and the long duration of winter nights. Day length  
168 duration at winter solstice was obtained from Garmin MapSource 6, considering the location  
169 coordinates of each study area. The latitudinal variation of the 26 study areas spanned 191 km  
170 or 1°47'02" (between 41°59'32" and 40°12'30"; Fig. 1). The daytime difference at winter  
171 solstice between the southernmost and northernmost localities was 12 minutes (547 vs. 559  
172 minutes). These small daily differences produced 13.5 h of accumulated day length throughout  
173 the study period between northern and southern localities.

174

#### 175 Data analyses

176 We used regression analyses and paired t-tests to describe between-winter changes in the study  
177 variables. Relationships between mean numbers of pellets per tree in 0.5-km transects  
178 and the predictor variables (bird abundance, cone abundance, tree density, air  
179 temperature, and day length) of the 26 studied juniper woodlands were explored by  
180 generalized linear regression models (canonical distribution: normal; link function:  
181 identity), using the information-theoretic model comparison approach. Alternative models  
182 were compared with Akaike's second-order AIC corrected for small sample sizes (AICc;  
183 Burnham and Anderson 2002). We introduced a quadratic term of tree cover into models to

184 check for nonlinearity in the influence of this predictor variable. Rather than base inferences on  
185 a single, selected best model from an a priori set of models, inference was based on the entire  
186 set of models using weights ( $W_i$ ) derived from AICc figures. This approach has both practical  
187 and philosophical advantages, as it is based on the Kullback-Leibler information theory. A  
188 model-averaged estimator is a more honest measure of precision and reduced bias compared to  
189 the estimator from just the selected best model (Burnham and Anderson 2004). Standardized  
190 regression coefficients ( $\beta$ ) were obtained in regression analyses as a measure of the sign and  
191 magnitude effects of predictor variables (i.e., analyses were carried out with standardized  
192 variables, such that their averages are zero and variances are 1). Parameter estimates ( $\beta$  and  $R^2$ )  
193 were averaged using model weights ( $W_i$ ) derived from all models with  $\Delta AICc \leq 4$ . Number of  
194 thrush pellets, fruits and birds were included in analyses using ln-transformation. All the  
195 statistical analyses were carried out using Statistica 10 (StatSoft Inc, Tulsa, Oklahoma).

196         Residuals of regression models for both winters showed non-significant patterns  
197 of spatial autocorrelation ( $P > 0.2$ ) for between-woodland distances shorter than 48 km  
198 or longer than 101 km, with relative Moran's I figures ( $I/I_{\max}$ ) ranging between [-0.32,  
199 0.27] and [-0.25, 0.2] respectively (analyses carried out with SAM package, Rangel et  
200 al. 2010). There was a significant negative autocorrelated pattern in the residuals of the  
201 regression model of the first winter between 48-75 km ( $I/I_{\max} = -0.36$ ,  $P = 0.015$ ), and in  
202 the residuals of the second winter between 75-101 km ( $I/I_{\max} = -0.37$ ,  $P = 0.030$ ).

203 Therefore, there was not a clear spatial structure in the data after considering the  
204 ecological predictors we can link to functional hypotheses regarding the biological  
205 processes under study, and we can assume that the 26 woodlands are nearly independent  
206 samples with a complete lack of spatial autocorrelation among nearer woodlands.

207         Day length was not significantly correlated with any other explanatory variable  
208 (absolute value of  $r$  with the other seven predictors  $< 0.3$ ,  $P > 0.15$ ). Altitude showed a  
209 relatively low variation among localities (maximum of 364 m; Table 1) and was only



210 significantly correlated with thrush abundance during winter 2009-2010 ( $r = -0.446$ ,  $P =$   
211  $0.022$ ), although its significance faded after applying Bonferroni's correction for  
212 multiple  $p$ 's estimations. Therefore, both altitude and day length were loosely related to  
213 other explanatory variables. We decided to remove altitude from statistical analyses in  
214 order to avoid the expected collinearity with temperature.

215

216

## 217 **Results**

218 The winter of 2009-2010 was colder than the winter 2010-2011, with average minimum  
219 temperatures below zero in both cases (Table 1). Both winters also differed in cone crop, with  
220 the second winter having six times more ripe cones than the first one (Table 1). In the winter  
221 2010-2011, many migratory thrushes arrived at the range of the juniper woodlands (e.g. *T.*  
222 *pilaris*, *T. iliacus*, *T. philomelos*) where increased local populations of blackbirds (*T. merula*)  
223 and Mistle thrushes (*T. viscivorus*). Globally, the increase in thrush and pellet numbers was two-  
224 times lower than the increase recorded in cone abundance (Table 1). Cone and thrush  
225 abundance were only significantly correlated in the second winter 2010-2011 of high  
226 fruit availability ( $r = 0.463$ ,  $P = 0.017$ ); the association between these two variables was  
227 considerably lower in the first winter with six times less ripe cones ( $r = 0.172$ ,  $P =$   
228  $0.400$ ).

229 The Akaike multimodel inference supported a prominent role for thrush abundance and  
230 day length in the geographical distribution of pellet abundance during the two study winters  
231 (Table 2, Fig. 2). In addition, cone abundance correlated with pellet abundance during the  
232 second winter and, in the colder winter 2009-2010, minimum temperatures depicted a weak,  
233 negative relationship with the spatial patterning of pellets (Table 2). The remaining predictor  
234 variables had a low strength of evidence and magnitude effects (sum of Akaike weights  $< 0.27$   
235 and absolute values of weighted standardized  $\beta$  regression coefficients  $< 0.10$ ; Table 2). The

236 percentages of explained variance in pellet abundance were 34% and 70%, respectively, in  
237 2009-2010 and 2010-2011 winters (weighted average of  $R^2$  using model weights  $W_i$  in Table 2).

238

## 239 **Discussion**

240 Effect of thrush abundance on pellet rain

241 Thrushes tracked inter-winter changes in ripe cones, but their ability to adjust numbers  
242 to fruit resources seemed rather crude during the study period. Despite there being a six-fold  
243 average increase in ripe cones in the second winter, there was a three-fold increase in thrush and  
244 pellet numbers (Table 1). This decoupling may result from asynchrony between some intrinsic  
245 (e.g., annual conditions affecting flowering and cone production of juniper woodlands) and  
246 extrinsic, large-scale features affecting the Spanish juniper woodlands. For instance, uncoupling  
247 between cone and bird abundance in juniper woodlands may result from annual variations in the  
248 breeding success of thrushes in nesting areas, or unexpected weather hazards (e.g., cold waves)  
249 affecting the displacements of migratory birds at the scale of Western Europe (Herrera 1998).  
250 Interestingly, the breeding populations of migratory thrushes arriving to winter in Iberia did not  
251 show any increase in 2010 (European Bird Census Committee, (<http://www.ebcc.info/bcn.html>)  
252 and the only continental cold-wave detected during the period occurred in winter 2009-2010  
253 (Cohen et al. 2010). Therefore, it seems less likely that annual variations in the breeding success  
254 and weather hazards caused the sharp increase of wintering thrushes in the winter 2010-2011.

255 Spanish juniper woodlands are just one of the several possible wintering habitats  
256 occupied by thrushes in the Iberian Peninsula, where they move in search of food over large  
257 distances (Santos 1982; Jordano 1993; Rey 1995). This means that the selection by most  
258 thrushes of alternative wintering habitats at the scale of the Iberian Peninsula might produce an  
259 unbalanced bird distribution with regards the extant annual cone availability of the Spanish  
260 juniper woodlands. However, despite these contingent large-scale effects on thrush abundance,  
261 results suggests that the large production of cones during the second winter attracted many  
262 thrushes and that this increase in thrush regional population resulted in thrushes producing seed  
263 rain according to spatial variation in cone abundance among juniper woodlands. This suggests a

264 density-dependent process of habitat occupation in which thrushes increased their ability to  
265 track variation in cone abundance when the regional populations were large enough to allocate  
266 individuals according to their extant availability of ripe cones (Tellería et al. 2008, 2013).  
267 Therefore, at the scale of the Spanish juniper-thrush system of the Iberian highlands, the call  
268 effect of high cone production on migratory thrushes may be interpreted as a driver of their  
269 ability to disperse seeds according to the geographical patterning of ripe cone abundance (see,  
270 however, Kelly and Sork 2002).

271

272 Effects of vegetation structure, temperature and day-length on pellet rain

273 Tree cover and temperature showed little effects on seed rain produced by thrushes.  
274 Despite the broad range in tree density (46 to 440 trees / ha; Table 1) no significant effect was  
275 detected during the two study winters suggesting that seed dispersion by thrushes within the  
276 range of the Spanish juniper woodlands was not related at all with tree cover. Temperature  
277 depicted a similar result (low sum of Akaike weights and standardized regression coefficients,  
278 Table 2), despite the fact that they were under the lower critical temperature for birds (around  
279 20°C; Calder and King 1974; Table 1). The detected variation of around 2.5 °C among localities  
280 was not enough to produce changes in pellet deposition resulting from potential changes in food  
281 requirements (Kwit et al. 2004).

282 Daylight was a main correlate of pellet abundance during the two study winters (Table  
283 1). The most parsimonious explanation for the effect of day length on pellet rain abundance is  
284 that it depicts geographical differences in the time available to feed (Sanz et al. 2000; Carrascal  
285 et al. 2012). In our study area, the average difference in day length between the northern- and  
286 southern-most localities is 10.5 minutes per day. This average difference accumulated over 90  
287 winter days (December-January-February) amounts to 16 h of daytime that is available for  
288 foraging in southernmost localities if compared to the northernmost ones. Thrushes are able to  
289 regurgitate seeds shortly after ripe cones are ingested by rapid elimination of non-nutritional  
290 remains that occupy space in the gut (Sorensen 1984; Levey 1987). This means that if they use  
291 most of this additional time to feed (e.g., to cope with energy requirements of long winter

292 nights), they will produce a significant increase in pellets delivered in those woodlands with  
293 longer day lengths (i.e., southern localities). Active search for ripe cones could be related to  
294 their high content of metabolized nonstructural carbohydrates (Herrera 1987), one of the most  
295 suitable foods to face energetic requirements (Jordano 1993). Consequently, geographical  
296 variation in day length introduces a time budget component of bird biology associated with  
297 latitude (Carrascal et al. 2012) whose explicit effect and frugivore-fruit interactions merit  
298 further investigation.

299

### 300 Conclusions

301 This study is a snapshot of a large-scale process related to the role of thrushes in the  
302 reproductive biology of the Spanish juniper. It shows that the links between the spatial  
303 variation of cone production and the distribution of seed dispersion activity by thrushes,  
304 as reflected by pellet abundance within the woodlands, may be distorted by their  
305 inability to track cone abundance in a year with less cones. Lack of dispersal activity  
306 may disrupt the transition from fruit to seedling within the reproductive cycle of  
307 junipers and may affect, along other features (e.g., microsite quality for germination and  
308 growth, seed predation, etc.) seed dispersal effectiveness of plant populations (Schupp  
309 et al. 2010). It is important to realize, however, that dispersal effectiveness of the  
310 Spanish junipers is far from being controlled by the thrushes alone, since other  
311 vertebrates (e.g. mammals) may also feed on ripe cones and disperse the seeds (e.g.  
312 mammals; Santos et al. 1999, Escribano-Ávila et al. 2012).

313         Despite the need for long-term investigations on this topic within a more complex  
314 conceptual framework (seed dispersal effectiveness must be quantified as the  
315 number of seeds dispersed by dispersal agents multiplied by the probability that dispersed seeds  
316 produce a new adult; Schupp et al. 2010), empirical evidence provided in this study suggests  
317 three main conclusions that may be used to launch further approaches to this process. First,  
318 results clearly report the changing role of thrushes on the geographical distribution of seed rain

319 within the range of the Spanish juniper (Myers and Harms 2009). Second, seed dispersion  
 320 among woodlands appears strongly dependent on some large-scale features affecting bird  
 321 numbers (e.g. the arrival of extra-Iberian migratory birds) and feeding behaviour (e.g. day  
 322 length duration), a pattern that shows a primary role for variables acting at larger scales on local  
 323 fruit-frugivore interaction (García et al. 2011). Finally, these results also support the promising  
 324 perspectives of considering large-scale approaches to exploring the drivers of some ecological  
 325 processes (Jenkins and Ricklefs 2011).

326

327 **Acknowledgements** This paper, funded by project CGL2008-2011/BOS of the Spanish  
 328 Ministry of Economy and Competitiveness, is a contribution to the International Campus of  
 329 Excellence launched by Complutense University of Madrid (UCM), Polytechnic University of  
 330 Madrid (UPM) and the Spanish Council for Scientific Research (CSIC). Two anonymous  
 331 reviewers considerably improved an early version of this paper. We are grateful to Claire  
 332 Jasinski and Sarah Young for improving the English of the manuscript.

333

### 334 **References**

- 335 Alcántara JM, Rey PJ, Valera F, Sánchez-Lafuente AM (2000) Factors shaping the seedfall  
 336 pattern of a bird-dispersed plant. *Ecology* 81: 1937-1950.
- 337 Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical  
 338 information–theoretic approach. 2nd edn. Springer-Verlag.
- 339 Burnham KP, Anderson DR (2004) Multimodel inference: Understanding AIC and BIC model  
 340 selection. *Sociol. Method. Res.* 33: 261-304
- 341 Calder WA, King JR (1974) Thermal and caloric relations of birds. In: Farner DS, King JR  
 342 (eds) *Avian Biology*, Vol. 4. Academic Press, New York. pp 259–413
- 343 Carrascal LM, Santos T, Tellería JL (2012) Does day-length affect winter bird distribution?  
 344 Testing the role of an elusive variable in crested tits inhabiting juniper woodlands.  
 345 *PlosOne* 7: e232733. DOI 10.1371/journal.pone.0032733

- 346 Cohen J, Foster J, Barlow M, Saito K, Jones J (2010). Winter 2009–2010: A case study of an  
347 extreme Arctic Oscillation event. *Geophysical Research Letters* 37: L17307.
- 348 Escribano-Avila G, Sanz-Pérez V, Pías B, Virgós E, Escudero A, Valladares, F (2012)  
349 Colonization of Abandoned Land by *Juniperus thurifera* Is Mediated by the Interaction  
350 of a Diverse Dispersal Assemblage and Environmental Heterogeneity. *Plos One*  
351 7(10):e46993. DOI 10.1371/journal.pone.0046993
- 352 Escribano-Avila G, Sanz-Pérez V, Pías B, Virgós E, Escudero A, Valladares, F (2012)  
353 Colonization of Abandoned Land by *Juniperus thurifera* Is Mediated by the Interaction  
354 of a Diverse Dispersal Assemblage and Environmental Heterogeneity. *Plos One*  
355 7(10):e46993
- 356 Fretwell SD (1972) *Populations in a seasonal environment*. Princeton University Press, New  
357 Jersey
- 358 García D, Ortiz-Pulido R (2004) Patterns of resource tracking by avian frugivores at multiple  
359 spatial scales: two case studies on discordance among scales. *Ecography* 27:187- 196.
- 360 García D, Zamora R, Amico GC (2011) The spatial scale of plant–animal interactions: effects of  
361 resource availability and habitat structure. *Ecol Monogr* 81: 103–121.
- 362 Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH (2000)  
363 Abundance– occupancy relationships. *J Appl Ecol* 37:39–59.
- 364 Herrera CM (1987) Vertebrate-dispersed plants of the Iberian peninsula: A study of fruit  
365 characteristics. *Ecol Monogr* 57:305-331.
- 366 Herrera CM (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a  
367 12-year study. *Ecological Monographs* 68: 511-538.
- 368 Herrera CM (2002) Seed dispersal by vertebrates. In: Herrera CM, Pellmyr O (eds)  
369 *Plant–animal interactions: an evolutionary approach*. Blackwell, Oxford, pp. 185-208
- 370 Herrera JM, García D (2010) Effects of forest fragmentation on seed dispersal and seedling  
371 establishment in ornithochorous trees. *Conservation Biology* 24: 1089–1098.
- 372 Holl KD (1998) Do bird perching structures elevate seed rain and seedling establishment in  
373 abandoned tropical pasture? *Rest. Ecol.* 6: 253–261

- 374 Hutto RT (1985) Habitat selection by non-breeding migratory landbirds. In: Cody ML (ed)  
375 Habitat selection in birds. Academic Press, Orlando, pp 455-476
- 376 Jenkins DG, Riklefs RE (2011) Biogeography and ecology: two views of one world. Philos.  
377 Trans. R. Soc. Lond. B Biol. Sci. 366: 2331–2335.
- 378 Jordano P (1993) Geographical ecology and variation of plant-seed disperser interactions:  
379 southern Spanish junipers and frugivorous thrushes. *Vegetatio* 107-108: 85-93
- 380 Jordano P (2000) Fruits and frugivory. In: Fenner M (ed) *Seeds: the ecology of regeneration in*  
381 *plant communities*. CABI Publishing, Wallingford. pp. 125-166.
- 382 Jordano P, Godoy JA (2002) Frugivore-generated seed shadows: a landscape view of  
383 demographic and genetic effects. In: Levey DJ, Silva WR, Galetti M (eds) *Seed*  
384 *dispersal and frugivory: ecology, evolution and conservation*. CABI Publishing,  
385 Wallingford. pp 305-323.
- 386 Kelly D, Sork VL (2002) Mast Seeding in Perennial Plants: Why, How, Where? *Annual Review*  
387 *of Ecology and Systematics* 33: 427-447.
- 388 Kollmann J (2000) Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspectives in*  
389 *Plant Ecology, Evolution and Systematic* 3: 29–51.
- 390 Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical  
391 framework for the study of heterogeneity. *Oikos* 59:253–260. DOI 10.2307/3545542
- 392 Kwit C, Levey DJ, Greenberg CH, Pearson SF, McCarty IP, Sargent S (2004) Cold temperature  
393 increases winter fruit removal rate of a bird-dispersed shrub. *Oecologia* 139: 30–34.
- 394 Levey DJ (1987) Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* 29: 471-  
395 485.
- 396 Levey DJ, Silva WR, Galetti M (2002) *Seed Dispersal and Frugivory: Ecology, Evolution and*  
397 *Conservation*. CAB International, Wallingford
- 398 Levey, DJ, Stiles FG (1992) Evolutionary precursors of long-distance migration: resource  
399 availability and movement patterns in Neotropical landbirds. *Am Nat* 140: 447-476.
- 400 Montesinos D (2007) *Juniperus thurifera*: una especie dioica, vecera y relictica. *Ecosistemas*  
401 16: 172-185.

- 402 Myers JA, Harms KE (2009) Seed arrival, ecological filters, and plant species richness: a meta-  
403 analysis. *Ecology Letters* 12: 1250-1260.
- 404 Ninyerola M, Pons X, Roure JM (2005) Atlas climatológico digital de la península  
405 Ibérica..Metodología y aplicaciones en bioclimatología y geobotánica. Universidad  
406 Autónoma de Barcelona. Bellaterra.
- 407 Rangel TF, Diniz-Filho JAF, Bini LM (2010) SAM: a comprehensive application for  
408 Spatial Analysis in Macroecology. *Ecography* 33: 46-50.
- 409 Rey PJ (1995) Spatio-temporal variation in fruit and frugivorous bird abundance in olive  
410 orchards. *Ecology* 76:1625-1635.
- 411 Root TL (1988) Energy constraints on avian distributions and abundances. *Ecology* 69: 330-  
412 339.
- 413 Santos T (1982) Migración e invernada de zorzales y mirlos (género *Turdus*) en la Península  
414 Ibérica. PhD dissertation. Department of Zoology, Universidad Complutense, Madrid.
- 415 Santos T, Suárez F, Tellería JL (1983) The bird communities of Iberian Juniper woodlands  
416 (*Juniperus thurifera* L.). In Purroy FJ (ed) Bird Census and Mediterranean Landscape.  
417 Editorial de la Universidad de León, León, pp. 79-88
- 418 Santos T, Tellería JL, Virgós E (1999) Dispersal of Spanish Juniper *Juniperus thurifera* by birds  
419 and mammals in a fragmented landscape. *Ecography* 22: 193-204.
- 420 Sanz JJ, Tinbergen JM, Moreno J, Orell M, Verhulst S (2000) Latitudinal variation in parental  
421 energy expenditure during brood rearing in the great tit. *Oecologia* 122: 149–154.
- 422 Schupp EW (1993) Quantity, quality and effectiveness of seed dispersal by animals. *Vegetatio*  
423 107/108: 15–29.
- 424 Schupp EW, Jordano P, García JM (2010) Seed dispersal effectiveness revisited. *New Phytol*  
425 188:333-353.
- 426 Sorensen AE (1984) Nutrition, energy, and passage times: experiments with fruit preference in  
427 European blackbirds. *J. Anim. Ecol.* 53: 545-557.



- 428 Tellería JL, de la Hera I, Ramírez A, Santos T (2011) Conservation opportunities in Spanish  
429 juniper *Juniperus thurifera* woodlands: the case of migratory thrushes *Turdus* spp.  
430 *Ardeola* 58:57-60
- 431 Tellería JL., Ramírez A, Pérez Tris J (2008) Fruit tracking between sites and years by birds in  
432 Mediterranean wintering grounds. *Ecography* 31:381-388.
- 433 Tellería JL, Carrascal LM, Santos, T (2013) Species abundance and migratory status affects  
434 large-scale fruit tracking in thrushes (*Turdus* spp.). *J Ornithol*: DOI  
435 10.1007/s10336-013-0997-5
- 436 Wenny DG (2001) Advantages of seed dispersal: A re-evaluation of directed dispersal.  
437 *Evolutionary Ecology Research* 3: 51–74.

438 **Table 1** Mean ( $\pm$  SE) of the study variables in 26 juniper woodlands in Spain during two consecutive winters.

	Winter 2009-2010	Winter 2010-2011	Paired t-tests
	mean $\pm$ se (min-max)	mean $\pm$ se (min-max)	
Number of birds per transect			
Blackbird ( <i>Turdus merula</i> )	0.5 $\pm$ 0.1 (0-2.3)	0.8 $\pm$ 0.1 (0-2.3)	t = 2.10 P = 0.046
Mistle thrush ( <i>Turdus viscivorus</i> )	2.4 $\pm$ 0.8 (0-17.3)	2.7 $\pm$ 0.4 (0.3-8.3)	t = 1.75 P = 0.093
Fieldfare ( <i>Turdus pilaris</i> )*	0.3 $\pm$ 0.2 (0-6.0)	2.9 $\pm$ 2.5 (0-64.3)	t = 1.25 P = 0.222
Redwing ( <i>Turdus iliacus</i> )*	0.6 $\pm$ 0.3 (0-7.0)	2.9 $\pm$ 1.5 (0-39.0)	t = 2.60 P = 0.016
Ring ouzel ( <i>Turdus torquatus</i> )*	-	0.1 $\pm$ 0.1 (0-1.0)	-
Song thrush ( <i>Turdus philomelos</i> )*	0.0 $\pm$ 0.0 (0-0.3)	1.8 $\pm$ 0.5 (0-8.7)	t = 4.75 P < 0.001
Total number of thrushes per transect	3.6 $\pm$ 1.1 (0.0-18.7)	11.2 $\pm$ 4.0 ( 1.0-107.7)	t = 3.50 P = 0.002
Number of pellets	10.4 $\pm$ 3.4 (0-63.9)	34.9 $\pm$ 5.9 (1.7-108.5)	t = 5.41 P < 0.001
Number of ripe fruits per tree	102.5 $\pm$ 42.4 (0-1018.6)	611.1 $\pm$ 150.3 (2.1-3098.0)	t = 6.06 P < 0.001
Minimum night temperature (°C)	-1.7 $\pm$ 0.1 (-3.2/-0.8)	-1.1 $\pm$ 0.2 (-3.2-0.3)	t = 5.07 P < 0.001
Day length (minutes)	553.1 $\pm$ 0.8 (547-559)		
Tree density (ha <sup>-1</sup> )	197.0 $\pm$ 19.8 (46-440)		
Altitude (m)	1176 $\pm$ 19.8 (950-1314)		

439 *Notes:* Relative abundance of thrushes refers to the average number of birds counted in three 500 m transects without detection distance limits per  
440 winter. Number of pellets: average number of pellets found under the tree crown of ten junipers in each woodland. Number of ripe fruits per tree:  
441 average number of ripe fruits in 50 (2009-2010) and 20 (2010-2011) randomly selected juniper trees in each woodland. Values for temperatures are  
442 averages for 77 days (1<sup>st</sup> December to 15<sup>th</sup> February) in the two consecutive winters. Day length and tree cover are variables that did not change  
443 between years. Paired t-test: results of paired t-tests comparing the two winters using the 26 juniper woodlands (d.f. = 25 in all tests). Asterisks (\*) show  
444 those species without breeding populations in juniper woodlands.

445 **Table 2** Alternative models for the relative abundance of thrush pellets in juniper woodlands of  
 446 Spain during the winters of 2009-2010 and 2010-2011 ordered by the value of the AICc  
 447 criterion (AIC corrected for small sample sizes).

Winter 2009-2010										
model	$W_i$	AICc	$R^2$	regression coefficient ( $\beta$ )						
				Day length	Tree density	Tree density <sup>2</sup>	Tmin	#Fruit	#Thrush	
1	0.231	83.98	0.33	0.43	-	-	-	-	-	0.53
2	0.132	85.09	0.37	0.40	-	-	-0.21	-	-	0.50
3	0.085	85.98	0.35	0.39	-	-	-	0.15	-	0.49
4	0.084	85.99	0.35	0.34	-0.15	-	-	-	-	0.52
		mean $R^2$	0.34							
		mean $\beta$		0.32	-0.10	0.05	-0.10	0.04	0.48	
		$\Sigma W_i$		0.82	0.26	0.18	0.42	0.20	1.00	
Winter 2010-2011										
model	$W_i$	AICc	$R^2$	regression coefficient ( $\beta$ )						
				Day length	Tree density	Tree density <sup>2</sup>	Tmin	#Fruit	#Thrush	
1	0.312	56.94	0.71	0.62	-	-	-	0.34	0.29	
2	0.135	58.62	0.66	0.51	-	-	-	0.50	-	
3	0.121	58.83	0.73	0.59	-0.12	-	-	0.33	0.30	
4	0.119	58.88	0.72	0.56	-	-0.12	-	0.33	0.30	
		mean $R^2$	0.70							
		mean $\beta$		0.58	-0.02	-0.02	-0.02	0.36	0.22	
		$\Sigma W_i$		1.00	0.17	0.17	0.15	0.93	0.70	

448  
 449 *Notes:* Although multimodel inference has been carried out considering models with  $\Delta AICc \leq 4$   
 450 (15 models for winter 2009-2010 and 9 models for winter 2010-2011), only models with  
 451  $\Delta AICc \leq 2$  are shown for the sake of brevity.  $\beta$ : standardized regression coefficients  
 452 obtained in generalized linear model (beta figures inform about the magnitude and sign  
 453 of the partial relationships of the standardized figures of predictor variables with the  
 454 abundance pellets).  $W_i$ : model weight;  $\Sigma W_i$ : sum of Akaike weights for each variable  
 455 considering those models where they were selected. mean  $\beta$ : weighted averages of standardized  
 456 regression coefficients considering model weights  $W_i$ .  $R^2$ : variance explained by each model.  
 457 Tmin: average minimum night temperature in the time span 1<sup>st</sup> December to 15<sup>th</sup> February.  
 458 #Fruit: average number of ripe fruits in 20 randomly selected juniper trees. #Thrush: number of  
 459 thrushes counted in three 500 m transects.

460

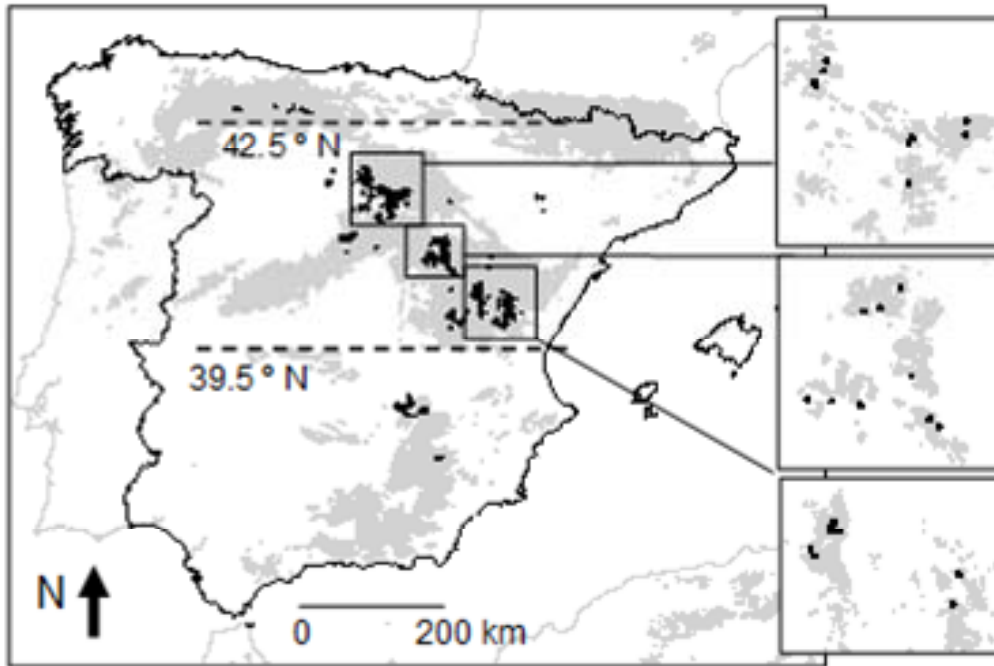
461 **Fig. 1** Distribution of Spanish juniper woodlands and location of the study sites. Grey  
462 tones depict areas over 1000 m above sea level and black patches show the actual  
463 distribution of the Spanish juniper woodlands. Boxes show the distribution of the study  
464 sites (black points) within the expanses of juniper woodlands (grey).

465

466 **Fig. 2** Relationship between the partial residuals of standardized values of pellet  
467 abundance and thrush abundance, ripe cone abundance, temperature and day length  
468 during the two study winters. Residual plots show the relationship between a given  
469 independent variable and pellet abundance given that the other three independent  
470 variables are also in the model, therefore partialling out their effects (i.e., building a  
471 model with pellet abundance as the response variable and thrush abundance, ripe cone  
472 abundance, temperature and day length as predictors). The linear and quadratic terms of  
473 tree density were excluded from the analyses of partial residual plots because their  $\Sigma W_i$   
474 were lower than 0.3 in both years (see Table 2). Dashed and solid lines represent the  
475 regression lines for the first (2009-2010) and second (2010-2011) winters, respectively.

476

477



478

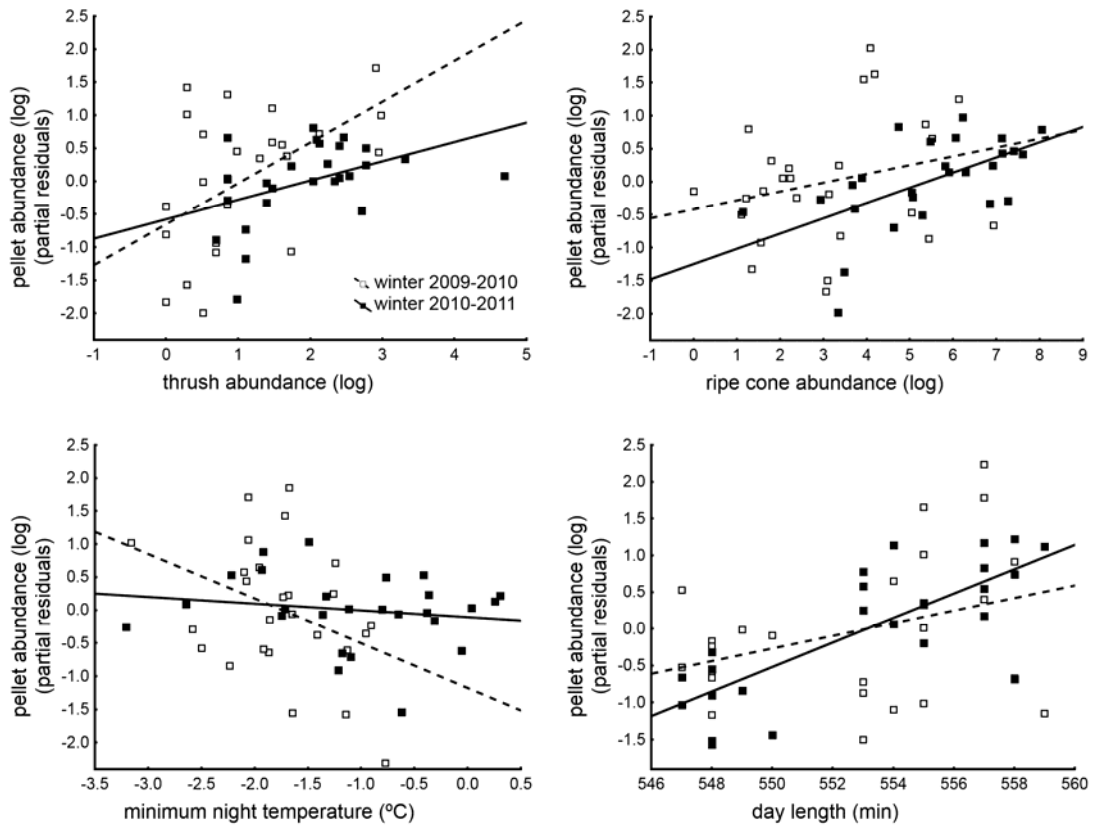
479

480 Fig.1

481

482

483



484

485 Fig.2