

1 **Seed dispersers help plants to escape global warming**

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12

13 *Abstract*

14 Plants are shifting their ranges towards higher elevations in response to global warming, yet
15 such shifts are occurring at a rate slower than is needed to keep pace with a rapidly changing
16 climate. There is, however, an almost complete lack of knowledge on seed dispersal across
17 altitude, a key process to understand what constrains climate-driven range shifts. Here, we
18 report the first direct empirical evidence on altitudinal seed dispersal mediated by two
19 common frugivorous mammals: the red fox *Vulpes vulpes* and the pine marten *Martes*
20 *martes*. We conducted a 3-year (bait-marking) experiment in a mountainous region of Spain.
21 We offered experimental fruits containing colour-coded seed mimics at feeding stations that
22 simulated source trees. The colour codes allowed us to identify the exact origin of seed
23 mimics found later in mammal scats. Nearly half (47%) of the dispersal events occurred
24 towards higher elevations, despite only ca. 25% of the study area being above the average
25 altitude of the feeding stations (1344 m). Seeds dispersed uphill gained an average of 106 m
26 (median = 111 m) and a maximum of 288 m, greatly exceeding the estimated requirements to
27 escape warming (35.4 m per decade). Yet, foxes mediated much more uphill seed dispersal
28 than martens (57% and 26% of dispersal events, respectively), which can be explained by
29 between-disperser differences in home range size and habitat specificity. Dispersers with
30 larger home ranges move farther and potentially disperse more seeds to higher altitudes,
31 while habitat generalism is necessary to transport seeds above vegetation belts delimiting
32 contrasting habitat types. We discuss how both traits (home range size and habitat specificity)
33 can be used to infer altitudinal seed dispersal across disperser species and mountainous
34 landscapes.

35

36

37 **Introduction**

38 As a result of global warming, many plant and animal species are shifting their ranges
39 worldwide, generally moving towards the poles and higher altitudes (Parmesan 2006, Chen et
40 al. 2011, Devictor et al. 2012, Lenoir and Svenning 2015). A critical question is whether
41 species will be able to disperse fast enough to track their suitable climatic ranges (Pearson
42 2006, Jump et al. 2009, Ozinga et al. 2009, Chen et al. 2011, Devictor et al. 2012, Schloss et
43 al. 2012, Cunze et al. 2013). Answering this question is key for both predicting the impacts of
44 global warming on ecosystems and understanding the role of dispersal limitation in
45 determining novel communities (Ozinga et al. 2009, Schloss et al. 2012).

46 Plants are sessile organisms and seeds (or spores in ferns) constitute the unique
47 mobile stage during the life of individuals. Given the long seed dispersal distances required to
48 track climate change in latitude (Hampe 2011, McConkey et al. 2012, Corlett and Westcott
49 2013, Cunze et al. 2013), altitudinal migration in mountainous regions has been suggested to
50 be the most feasible shortcut to keep pace with rapidly changing climate (Colwell et al. 2008,
51 Jump et al. 2009): an altitudinal shift of 100 m corresponds, in climatic terms, to roughly a
52 100-km shift in latitude (Colwell et al. 2008). A recent global meta-analysis of observed
53 range shifts found a median altitudinal increase of 16.0 m per decade in plants, less than half
54 the estimated 35.4 m per decade needed to track rising temperatures (Chen et al. 2011).
55 Nonetheless, empirical evidence on altitudinal seed dispersal has been completely lacking
56 until recently, when Naoe and colleagues (2016) inferred – through an indirect, isotope-based
57 method – extensive uphill seed dispersal (hundreds of meters) in the cherry tree *Prunus*
58 *verecunda* in Japan. Although other approaches, such as transplant experiments, can help us
59 to infer the presence or absence of dispersal limitation (Lee-Yaw et al. 2016), knowledge of
60 the seed dispersal process is essential to understand the observed range shifts and predict
61 future changes (Neilson et al. 2005, Hampe 2011).

62 Many plants across the world's biomes depend on animals to disperse their seeds
63 (Jordano 2013). Their ability to reach higher altitudes will ultimately depend on the
64 movement patterns of the disperser species they interact with (Jordano et al. 2007, González-
65 Varo et al. 2013). During the last decade there have been significant advances in our
66 understanding of seed dispersal distances in the horizontal plane mediated by different animal
67 taxa (Jordano et al. 2007, Spiegel and Nathan 2007, González-Varo et al. 2013, Pérez-
68 Méndez et al. 2016). For example, we know that many bird and mammal species regularly
69 disperse seeds at distances ranging from a few hundred meters to a few kilometers (Jordano
70 et al. 2007, Spiegel and Nathan 2007, González-Varo et al. 2013). However, seed dispersal in
71 the vertical axis, such as when dispersers occur in a mountainous region, remains an issue.
72 We therefore asked the question: do seed dispersers help plants by providing the estimated
73 elevational displacements they need to track their suitable climatic ranges?

74 Here we provide the first direct (i.e. non-correlational) empirical evidence of
75 altitudinal seed dispersal mediated by animals. We used an exceptional dataset resulting from
76 a 3-year field experiment carried out in a mountainous landscape in NW Spain, which aimed
77 at measuring seed dispersal events mediated by two common and widespread mammals: the
78 red fox (*Vulpes vulpes*, Canidae) and the pine marten (*Martes martes*, Mustelidae). Foxes
79 occur in North America, Eurasia, North Africa and Australia (non-native species), while
80 martens occur in Europe and Western Asia (Wilson and Mittermeier 2009). Both mammals
81 are important generalist frugivores and legitimate seed dispersers of many fleshy-fruited
82 species across plant communities, i.e. they transport seeds in their guts and defecate them in
83 conditions that are suitable for germination in different habitats and landscapes (Herrera
84 1989, De Marinis and Masseti 1995, Rosalino and Santos-Reis 2009, López-Bao and
85 González-Varo 2011, López-Bao et al. 2015). Our field (bait-marking) experiment consisted
86 of offering fruits containing colour-coded seed mimics to these mammals, at feeding stations

87 simulating source trees. The exclusive colour code of each simulated source tree allowed us
88 to locate the exact origin of seed mimics found later in fox and marten scats (González-Varo
89 et al. 2013), thereby directly measuring altitudinal seed dispersal using geo-referenced
90 information. Furthermore, we explore, for the first time, relationships between horizontal (x ,
91 y) and altitudinal (z) seed dispersal distances, and show the importance of habitat generalism
92 for dispersing seeds from forest habitats to deforested mountaintops.

93

94 **Methods**

95 We measured altitudinal seed dispersal events of fleshy-fruited species mediated by foxes and
96 martens by means of a 3-year bait-marking experiment carried out in the Devesa da Rogueira
97 forest, located in Serra do Courel (42°37'N–7°05'W), a mountainous region (ca. 250 km²) in
98 NW Iberian Peninsula. The study site had 22% of area below 1000 m a.s.l., 60% between
99 1000 and 1400 m, and 18% above 1400 m a.s.l.. Percentages were calculated using QGIS v.
100 2.14.0 (Quantum GIS Development Team 2015) within a circle of 4-km radius centred in the
101 study area. Forest occupies approximately 50% of the territory in the study region and is
102 usually restricted to altitudes below ~1400 m (Munilla et al. 2008). Detailed information on
103 this experiment and the main characteristics of study area can be found in González-Varo et
104 al. (2013). Briefly, we offered experimental fruits containing coloured seed mimics to the two
105 mammal species in three different years (2008, 2009 and 2010). We used figs of the common
106 fig tree (*Ficus carica*) as experimental fruits (~50 mm diameter; Fig. S1). Seeds mimics were
107 coloured plastic beads of (mean) 2.6 mm diameter and 27.1 mg weight (Fig. S1), which is
108 within the modal range of wild seeds dispersed by both species in the study area (whole
109 range: from ~0.2 mm diameter in bilberry *Vaccinium myrtillus* to ~10 mm in blackthorn
110 *Prunus spinosa* (López-Bao et al. 2015)). In other mammal species (Asiatic black bears
111 *Ursus thibetanus*), gut passage time does not vary significantly between different seed

112 species and seed mimics (Koike et al. 2011). Therefore, we expect the dispersal events
113 reported here to be representative of how foxes and martens disperse fleshy-fruited seeds
114 naturally.

115 We prepared the experimental figs, using tweezers to embed the seed mimics in their
116 pulp (10 seeds per fig). The baiting was carried out between September and October of each
117 year, coinciding with the peak of the fruiting season of fleshy-fruited species in the study area
118 (López-Bao and González-Varo 2011). Every September, we set up ‘feeding stations’ where
119 we offered the experimental figs on the ground below the canopy of ‘simulated fruiting trees’
120 (Fig. S2). Each feeding station consisted of an area of $\sim 60 \text{ m}^2$ with a total of six feeders (trays
121 of $18 \times 12 \times 3 \text{ cm}$; Fig. S1). We geo-referenced each feeding station using the centroid of the
122 polygon generated by the spatial position of the six feeders. An exclusive colour code was
123 assigned to the seed mimics offered at each feeding station. In this manner, we were able to
124 directly identify the source (feeding station) of any seed mimics dispersed by foxes and
125 martens, and subsequently found in their scats. We set up a total of eight feeding stations ($n =$
126 3, 6 and 6 feeding stations in 2008, 2009 and 2010, respectively), with distances between
127 stations ranging between 280 m and 1760 m (Fig. S2; Table S1).

128 We offered a total of 1322 experimental figs (13,220 seed mimics) during the 3 years
129 of the experiment; on average, 165.3 figs per station. We monitored fruit removal from the
130 feeding stations and searched for mammal scats twice a week from September to November
131 in each of the three study years. We followed a sampling strategy that aimed to detect the
132 longest dispersal events. This strategy consisted of (i) the intensive sampling within a 2-km
133 radius around each feeding station, and (ii) additional sampling within a 1-km radius around
134 the farthest seed dispersal event from each feeding station, until no more seed mimics were
135 found in that extra buffer (see details in González-Varo et al. 2013). We searched for scats
136 along a network of paths of ~ 70 -km length over an area of $\sim 40 \text{ km}^2$ (altitudinal range 600–

137 1643 m a.s.l.), and accounting for an accumulated walking distance of ~900 km during the
138 study period (González-Varo et al. 2013). Previous studies have shown that the density of
139 faeces of these mammals is much higher along paths than through the natural vegetation
140 (Suárez-Esteban et al. 2013). We found and analyzed 2027 mammal scats during the whole
141 study period (641 in 2008, 888 in 2009 and 498 in 2010). We found mammal scats containing
142 seed mimics from all but one feeding station (7 out of 8), which was excluded owing to
143 disturbance by wild boars (see Table S1). We recovered and geo-referenced 98 scats
144 containing 665 seed mimics, 95 of which (containing 657 seed mimics) were identified to
145 belong to red foxes or pine martens (Fig. S1). We also assigned a macrohabitat category to
146 each scat, differentiating between forest and non-forest habitats. Remarkably, 9 of the 95
147 scats had seed mimics belonging to two different feeding stations (i.e. different colours; see
148 Fig. S1): seven from red foxes and two from pine martens. Therefore, the 95 scats actually
149 accounted for 104 seed dispersal events (i.e. ‘source–scat’ combinations), 70 and 34 mediated
150 by red foxes and pine martens, respectively, which effectively constitute the sample size of
151 this study. It is noteworthy that overall recapture rates were ~5%, which is above those
152 obtained from bird ringing and within the range of those obtained in butterfly tagging; a
153 discussion on the method can be found in González-Varo et al. (2013).

154 We tested for statistical differences between red foxes and pine martens in altitudinal
155 seed dispersal using Mann-Whitney U tests, and in their relative contribution to seed
156 dispersal towards higher elevations using a Chi-square test. We also used a Chi-square test to
157 assess differences between foxes and martens in their frequency of seed deposition in forest
158 *versus* non-forest habitats. We tested whether there was a relationship between Euclidean (x ,
159 y) and altitudinal (z) seed dispersal distance, and whether such a relationship differed between
160 disperser species. For this analysis, we added a negative sign to the Euclidean distances
161 belonging to dispersal events towards lower elevations, that is, to negative altitudinal

162 dispersal distances. We used two linear models with altitudinal dispersal distance as the
163 response variable and Euclidean distance as the explanatory variable. In one model we
164 additionally included disperser species as an explanatory variable (fixed factor). The
165 interaction between Euclidean distance and disperser species allowed us to test for
166 differences between disperser species in the slopes through which they dispersed seeds
167 altitudinally. We evaluated model fit according to R^2 values and the Akaike Information
168 Criterion (AIC) (Burnham and Anderson 2002). All analyses were performed using R v. 3.2.3
169 (R Development Core Team 2015).

170

171 **Results**

172 We offered the experimental fruits at elevations ranging between 1169 and 1395 m and
173 subsequently found dispersed seeds between 831 and 1580 m, a range 3.3 times larger (Fig.
174 1A). It is worth noting that the highest elevation point in the study area is at 1643 m a.s.l., just
175 63 m higher than the maximum altitude reached by the seed mimics. Nearly half of scats with
176 seed mimics (47.1%; 49 out of 104) were found at higher elevations than their respective
177 source trees, gaining a median of 111 m (mean = 106 m) and a maximum of 288 m in
178 altitude.

179 Altitudinal patterns of seed deposition differed between disperser species (Fig. 1). We
180 found significant differences between foxes and martens in both the altitude of seed
181 deposition (Mann-Whitney U test: $P < 0.001$; Table 1, Fig. 1A) and the altitudinal seed
182 dispersal distance (Mann-Whitney U test: $P = 0.003$; Table 1, Fig. 1B). Indeed, the
183 percentage of dispersal events towards higher elevations was more than two-fold higher in
184 the red fox (57.1%; 40 out of 70 events) than in the pine marten (26.5%; 9 out of 34 events)
185 (Chi-square test: $\chi^2 = 7.45$, $df = 1$, $P = 0.006$) (Fig. 1B). Moreover, foxes deposited 57% of

186 scats (36 out of 63) in non-forest habitats (mainly heathlands), while martens only deposited
187 6% (2 out of 32) in non-forest habitats, the vast majority (94%) being found in forest habitats
188 (Chi-square test: $\chi^2 = 20.83$, $df = 1$, $P < 0.001$).

189 Finally, we detected a general positive and significant relationship between the
190 Euclidean and the altitudinal dispersal distances (Table 2), indicating that seeds dispersed
191 farther are more likely to reach both higher and lower elevations (Fig. 2). Yet, the slope of
192 such relationship differed between disperser species, being two times steeper in the pine
193 marten than in the red fox (Fig. 2). Indeed, the linear model incorporating the disperser
194 species showed a better fit than the model that only included the Euclidean distance, in terms
195 of both R^2 and AIC (Table 2).

196

197 **Discussion**

198 Our results provide the first direct empirical evidence that seed dispersers can altitudinally
199 disperse seeds to elevations that greatly exceed the estimated median 35.4 m (range: 8.3–56.7
200 m) per decade needed to track rising temperatures (Chen et al. 2011). We found that nearly
201 half of the dispersal events observed were towards higher and colder places. This frequency
202 of uphill seed dispersal is remarkable because area generally decreases with altitude and, in
203 fact, only ca. 25% of the study landscape is above the average altitude of the feeding stations
204 (1344 m). Considering the general decrease of temperature with elevation (5.2–6.5°C per
205 1000 m) (Colwell et al. 2008), the reported movements entail differences of up to 1.5–1.9°C
206 mean temperature decrease in a single dispersal event (max. altitudinal distance = 288 m).
207 Importantly, seed dispersal upwards – as opposed to downwards – was constrained by the
208 altitudinal limits of the study area (Fig. 1A, Fig. 2). Therefore, altitudinal dispersal distances
209 above the maximum value reported here (288 m) would be expected without such constraint

210 (e.g. higher mountains or dispersal from lower elevations). Whether fleshy-fruited plants will
211 be able to migrate altitudinally at a proper velocity will depend on (i) the possibilities of
212 recruitment above the current climatic range, and (ii) the time they need to reach the
213 reproductive age. First, seeds dispersed above the currently suitable climatic range will find
214 an unsuitable environment that is forecasted to be suitable in two or three decades. Dispersal
215 towards climate microrefugia (i.e. areas that support locally favourable climates; Dobrowski
216 2011) may therefore be crucial. Second, many early successional species can reach the
217 reproductive age in a few years, however, forest trees may require a few decades (1–4;
218 Nathan et al. 2011). Our results provide basic information that could be used to understand
219 the importance of both factors (i.e. habitat suitability and time lag until maturation age) on
220 altitudinal range shifts at the community level, though this is beyond the scope of the present
221 study.

222 Our findings add to the indirect evidence recently provided by Naoe et al. (2016) on
223 altitudinal dispersal distances generated by Asiatic black bears and Japanese martens (*Martes*
224 *melampus*). In their study, Naoe et al. (2016) found a negative correlation between altitude
225 and the oxygen isotope ratios (^{18}O and ^{16}O) of *Prunus verecunda* seeds sampled from mother
226 plants, then used the regression lines to estimate altitudinal seed dispersal. In our study, the
227 possibility of linking horizontal and altitudinal dispersal distances (Fig 2), along with the
228 distribution of the vegetation in our study area (i.e. deforested mountain tops; Fig. S3; see
229 also López-Bao and González-Varo 2011) allowed us to disentangle two key traits that
230 enable animal species to promote altitudinal seed dispersal: home range size and habitat
231 specificity. First, home range size determines the spatial scale of seed dispersal patterns in the
232 horizontal plane (Spiegel and Nathan 2007, González-Varo et al. 2013, Naoe et al. 2016,
233 Pérez-Méndez et al. 2016) and, therefore, also in the vertical axis when the disperser's daily
234 movements occur in mountainous regions (Fig. 2). Compared to animals with small home

235 ranges, animals that frequently perform long displacements are expected to disperse more
236 seeds towards higher elevations. Home range sizes are positively associated with the
237 frequency of long-distance seed dispersal and, in general, with the disperser's body sizes
238 (Harestad and Bunnell 1979, Spiegel and Nathan 2007, González-Varo et al. 2013, Naoe et al.
239 2016, Pérez-Méndez et al. 2016). These patterns hold for our study species (González-Varo et
240 al. 2013): body weights in red foxes and pine martens are of 3–14 kg and 0.8–1.8 kg,
241 respectively, and their home ranges have 200–600 ha and 50–190 ha, respectively (Cavallini
242 1996, Dekker et al. 2001, Zalewski et al. 2004, Wilson and Mittermeier 2009, Moreno-Opo et
243 al. 2015). Hence, larger animals move farther and potentially disperse more seeds to higher
244 altitudes. The topographic features of the study area, with very steep slopes, lead to major
245 altitudinal movements even when the Euclidean dispersal distances were relatively short (<1
246 km; especially by pine martens). Yet, long-distance dispersal events (farther than 1 km) were
247 required to move up seeds above 200 m in altitude (Fig. 2). It is not difficult to envisage a
248 much more important role of long-distance seed dispersal in mountainous regions with
249 shallower slopes, where extensive horizontal movements are needed to gain a few meters in
250 altitude. Our findings suggest that it is possible to infer altitudinal seed dispersal by
251 combining topographical maps and available knowledge on horizontal seed dispersal
252 distances. However, because such knowledge is very limited at the species level, within
253 diverse disperser assemblages (Jordano et al. 2007), information on home-range size (more
254 accessible at the species level; e.g. Dennis and Westcott 2007) can be used to infer maximum
255 horizontal dispersal distances (see González-Varo et al. 2013) and, therefore, maximum
256 altitudinal dispersal distances.

257 Second, the differences in the observed seed dispersal patterns between foxes and
258 martens appear related with the habitat specificity of both species. The red fox is a habitat-
259 generalist species that can be found up to 4500 m above sea level, above the mountain tree

260 line (Wilson and Mittermeier 2009), and that occupies forests, heathlands and farmlands
261 across all the altitudinal levels of our study region (López-Bao and González-Varo 2011). In
262 contrast, the pine marten is a forest-specialist species (Wilson and Mittermeier 2009,
263 Balestrieri et al. 2016) and, indeed, its upper elevational limit throughout the western
264 Palearctic is the limit of deciduous and conifer forests (e.g. up to 2300 m in the Pyrenees;
265 Herrero et al. 2016). As previously mentioned, forest occupies approximately 50% of the
266 territory in the study region and is usually limited to altitudes below ~1400 m (Fig. S3).
267 Hence, the upper limit of the seeds mobilized by the martens basically reflects the upper limit
268 of the forest (see Fig. 1A). This is demonstrated by our finding that the vast majority of
269 marten scats (94%) were found in forest habitats and only a minor fraction was found in non-
270 forest habitats (6%). Forest dependence in pine martens can also explain why they dispersed
271 seeds through steeper slopes because, in our study area, forests are mostly confined to the
272 steepest hillsides below 1400 m (see Fig. S1; see also Fig. 1 in López-Bao and González-
273 Varo 2011). Conversely, habitat generalism could explain why the histogram for the red fox
274 is slightly skewed towards higher elevations (Fig. 1A), with a peak between 1400 and 1500
275 m, just around the forest limit, in areas where this generalist species can benefit from
276 foraging in different habitat types. In fact, habitat diversity has been reported to be higher
277 within the home range of red foxes than at the landscape scale (Cavallini and Lovari 1994).
278 Accordingly, fox scats were more evenly distributed between forest (43%) and non-forest
279 habitats (57%), as found in other systems (e.g. Rost et al. 2012). These results demonstrate
280 that habitat generalism is necessary to transport seeds above vegetation belts that delimit
281 contrasting habitat types, in the same way it is in fragmented landscapes for seed dispersal
282 beyond the remnant vegetation (González-Varo et al. 2017). Therefore, our findings provide
283 evidence that habitat specificity of seed dispersers is a critical trait in the context of
284 altitudinal range expansions.

285 The widespread distribution of red foxes and pine martens (Wilson and Mittermeier
286 2009), and their occurrence in natural and anthropogenic landscapes (López-Bao and
287 González-Varo 2011, Balestrieri et al. 2016), suggest that the patterns reported here are likely
288 to be common in other mountainous regions as well. Only in our study area, foxes and
289 martens disperse the seeds of, at least, 14 fleshy-fruited plant species (López-Bao et al. 2015).
290 Therefore, these mammals, and their close relatives, may be helping hundreds of plant
291 species to escape global warming across continents and biomes (Willson 1993, Koike et al.
292 2008, Rosalino and Santos-Reis 2009, González-Varo et al. 2015). More importantly, our
293 study reveals two disperser traits that allow generalization beyond the studied animals: home
294 range size and habitat specificity. We propose the use of both traits as a baseline to infer
295 altitudinal seed dispersal mediated by other animal taxa, thereby as the starting hypotheses
296 for future studies on this topic. Specifically, we hypothesize a more important role of long-
297 distance seed dispersal in regions where mountains have shallow slopes, and a more
298 important role of habitat specificity in regions with steep mountains. Therefore, our study not
299 only demonstrates that seed dispersers help plants to track their suitable climatic ranges in
300 altitude, but also provides new insights into how information on dispersers' traits and
301 landscape attributes can be combined to forecast climate-driven altitudinal range shifts.

302

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315

316 **References**

317 Balestrieri, A., et al. 2016. Modelling the distribution of forest-dependent species in human-
318 dominated landscapes: patterns for the pine marten in intensively cultivated lowlands. - PLoS
319 ONE 11: e0158203.

320 Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A
321 Practical-Theoretic Approach, 2nd edn. - Springer.

322 Cavallini, P. and Lovari, S. 1994. Home range, habitat selection and activity of the red fox in
323 a Mediterranean coastal ecotone. - Acta Theriologica 39: 279-287.

324 Cavallini, P. 1996. Variation in the social system of the red fox. - Ethol. Ecol. Evol. 8: 323-
325 342.

326 Chen, I.-C., et al. 2011. Rapid range shifts of species associated with high levels of climate
327 warming. - Science 333: 1024-1026.

328 Colwell, R. K., et al. 2008. Global warming, elevational range shifts, and lowland biotic
329 attrition in the wet tropics. - Science 322: 258-261.

330 Corlett, R. T. and Westcott, D. A. 2013. Will plant movements keep up with climate change?
331 - Trends Ecol. Evol. 28: 482-488.

332 Cunze, S., et al. 2013. Are plant species able to keep pace with the rapidly changing climate?
333 - PLoS ONE 8: e67909.

334 De Marinis, A. M. and Masseti, M. 1995. Feeding habits of the pine marten *Martes martes*
335 L., 1758, in Europe: a review. - 1995 7: 143-150.

336 Dekker, J. J. A., et al. 2001. A spatial analysis of a population of red fox (*Vulpes vulpes*) in
337 the Dutch coastal dune area. - J. Zool. 255: 505-510.

- 338 Dennis, A. and Westcott, D. A. 2007. Estimating dispersal kernels produced by a diverse
339 community of vertebrates. - In: Dennis, A., et al. (eds.), Seed dispersal: theory and its
340 application in a changing world. CAB International, pp. 201-228.
- 341 Devictor, V., et al. 2012. Differences in the climatic debts of birds and butterflies at a
342 continental scale. - Nature Clim. Change 2: 121-124.
- 343 Dobrowski, S. Z. 2011. A climatic basis for microrefugia: the influence of terrain on climate.
344 - Global Change Biol. 17: 1022-1035.
- 345 González-Varo, J. P., et al. 2013. Functional diversity among seed dispersal kernels generated
346 by carnivorous mammals. - J. Anim. Ecol. 82: 562-571.
- 347 González-Varo, J. P., et al. 2015. Frugivory and seed dispersal by carnivorous mammals:
348 functional traits. - Revista Ecosistemas 24: 43-50.
- 349 González-Varo, J. P., et al. 2017. Unravelling seed dispersal through fragmented landscapes:
350 Frugivore species operate unevenly as mobile links. - Mol. Ecol. 00: 000-000.
- 351 Hampe, A. 2011. Plants on the move: The role of seed dispersal and initial population
352 establishment for climate-driven range expansions. - Acta Oecol. 37: 666-673.
- 353 Harestad, A. S. and Bunnell, F. L. 1979. Home range and body weight – a reevaluation. -
354 Ecology 60: 389-402.
- 355 Herrera, C. M. 1989. Frugivory and seed dispersal by carnivorous mammals, and associated
356 fruit characteristics, in undisturbed Mediterranean habitats. - Oikos 55: 250-262.
- 357 Herrero, J., et al. 2016. *Martes martes*. The IUCN Red List of Threatened Species, p.
358 e.T12848A45199169.
- 359 Jordano, P., et al. 2007. Differential contribution of frugivores to complex seed dispersal
360 patterns. - Proceedings of the National Academy of Sciences of the United States of America
361 104: 3278-3282.
- 362 Jordano, P. 2013. Fruits and frugivory. - In: Gallagher, R. S. (ed.) Seeds: the ecology of
363 regeneration of plant communities. CABI, pp. 18-61.
- 364 Jump, A. S., et al. 2009. The altitude-for-latitude disparity in the range retractions of woody
365 species. - Trends Ecol. Evol. 24: 694-701.
- 366 Koike, S., et al. 2008. Frugivory of carnivores and seed dispersal of fleshy fruits in cool-
367 temperate deciduous forests. - Journal of Forest Research 13: 215-222.

- 368 Koike, S., et al. 2011. Estimate of the seed shadow created by the Asiatic black bear *Ursus*
369 *thibetanus* and its characteristics as a seed disperser in Japanese cool-temperate forest. -
370 *Oikos* 120: 280-290.
- 371 Lee-Yaw, J. A., et al. 2016. A synthesis of transplant experiments and ecological niche
372 models suggests that range limits are often niche limits. - *Ecol. Lett.* 19: 710-722.
- 373 Lenoir, J. and Svenning, J. C. 2015. Climate-related range shifts – a global multidimensional
374 synthesis and new research directions. - *Ecography* 38: 15-28.
- 375 López-Bao, J. V. and González-Varo, J. P. 2011. Frugivory and spatial patterns of seed
376 deposition by carnivorous mammals in anthropogenic landscapes: a multi-scale approach. -
377 *PLoS One* 6: e14569.
- 378 López-Bao, J. V., et al. 2015. Mutualistic relationships under landscape change: Carnivorous
379 mammals and plants after 30 years of land abandonment. - *Basic Appl. Ecol.* 16: 152-161.
- 380 McConkey, K. R., et al. 2012. Seed dispersal in changing landscapes. - *Biol. Conserv.* 146: 1-
381 13.
- 382 Moreno-Opo, R., et al. 2015. Is it necessary managing carnivores to reverse the decline of
383 endangered prey species? Insights from a removal experiment of mesocarnivores to benefit
384 demographic parameters of the Pyrenean capercaillie. - *PLOS ONE* 10: e0139837.
- 385 Munilla, I., et al. 2008. Long-term changes in the breeding bird assemblages of two woodland
386 patches in northwest Spain. - *Ardeola* 55: 221-227.
- 387 Naoe, S., et al. 2016. Mountain-climbing bears protect cherry species from global warming
388 through vertical seed dispersal. - *Curr. Biol.* 26: R315-R316.
- 389 Nathan, R., et al. 2011. Spread of North American wind-dispersed trees in future
390 environments. - *Ecol. Lett.* 14: 211-219.
- 391 Neilson, R. P., et al. 2005. Forecasting regional to global plant migration in response to
392 climate change. - *Bioscience* 55: 749-759.
- 393 Ozinga, W. A., et al. 2009. Dispersal failure contributes to plant losses in NW Europe. - *Ecol.*
394 *Lett.* 12: 66-74.
- 395 Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. - *Annual*
396 *Review of Ecology, Evolution, and Systematics* 37: 637-669.
- 397 Pearson, R. G. 2006. Climate change and the migration capacity of species. - *Trends Ecol.*
398 *Evol.* 21: 111-113.

- 399 Pérez-Méndez, N., et al. 2016. The signatures of Anthropocene defaunation: cascading
400 effects of the seed dispersal collapse. - Scientific Reports 6: 24820.
- 401 Rosalino, L. M. and Santos-Reis, M. 2009. Fruit consumption by carnivores in Mediterranean
402 Europe. - Mamm. Rev. 39: 67-78.
- 403 Rost, J., et al. 2012. Seed dispersal by carnivorous mammals into burnt forests: An
404 opportunity for non-indigenous and cultivated plant species. - Basic Appl. Ecol. 13: 623-630.
- 405 Schloss, C. A., et al. 2012. Dispersal will limit ability of mammals to track climate change in
406 the Western Hemisphere. - Proceedings of the National Academy of Sciences 109: 8606-
407 8611.
- 408 Spiegel, O. and Nathan, R. 2007. Incorporating dispersal distance into the disperser
409 effectiveness framework: frugivorous birds provide complementary dispersal to plants in a
410 patchy environment. - Ecol. Lett. 10: 718-728.
- 411 Suárez-Esteban, A., et al. 2013. Barriers or corridors? The overlooked role of unpaved roads
412 in endozoochorous seed dispersal. - J. Appl. Ecol. 50: 767-774.
- 413 Willson, M. F. 1993. Mammals as seed-dispersal mutualists in North America. - Oikos 67:
414 159-176.
- 415 Wilson, D. E. and Mittermeier, R. A. 2009. Handbook of the mammals of the world. Vol. 1.
416 Carnivores. - Lynx Editions.
- 417 Zalewski, A., et al. 2004. Mobility and home range use by pine martens (*Martes martes*) in a
418 Polish primeval forest. - Ecoscience 11: 113-122.
- 419

Table 1. Summary statistics of altitude of seed deposition and altitudinal seed dispersal distances mediated by red foxes and pine martens.

Disperser species	Altitude of seed deposition (m)				Altitudinal dispersal distance (m)			
	Mean	Median	Min.	Max.	Mean	Median	Min.	Max.
Red fox	1382	1378	910	1580	26	31	-465	288
Pine marten	1253	1260	831	1546	-67	-30	-438	255

Table 2. Results of the linear models relating altitudinal seed dispersal distance to Euclidean dispersal distance and disperser species (red fox or pine marten). Note that model incorporating the disperser species had a better predictive power (+15.6%) and was more informative ($\Delta AIC = 34$).

Model: <i>Altitudinal distance</i> ~	R ²	AIC	Variables	F	P
<i>Euclidean distance</i>	0.465	1267.1	Euclidean	90.4	< 0.001
<i>Euclidean dist. × Disperser species</i>	0.621	1233.1	Euclidean	127.6	< 0.001
			Disperser	17.4	< 0.001
			Euclidean × Disperser	26.6	< 0.001

Figure 1. Altitudinal seed dispersal patterns mediated by red foxes and pine martens. (A) Altitudinal distribution (%) of scats from red fox (left) and pine marten (right) containing colour-coded seed mimics ($n = 63$ and 32 scats containing 451 and 206 seed mimics, respectively). Dotted lines denote the altitudinal range of the feeding stations (i.e. the simulated ‘source trees’ of the seed mimics); solid lines denote the median altitude of the feeding stations belonging to the seeds dispersed by each species; red lines denote the maximum altitude in the study area. The forest limit in the study area is at ~ 1400 m altitude. (B) Distribution (%) of altitudinal dispersal distances, i.e. the altitudinal difference between the source and deposition sites of dispersed seed mimics ($n = 70$ and 34 dispersal events). The colour gradient is associated to 100-m altitudinal intervals in order to illustrate seed dispersal events towards colder and warmer ranges.

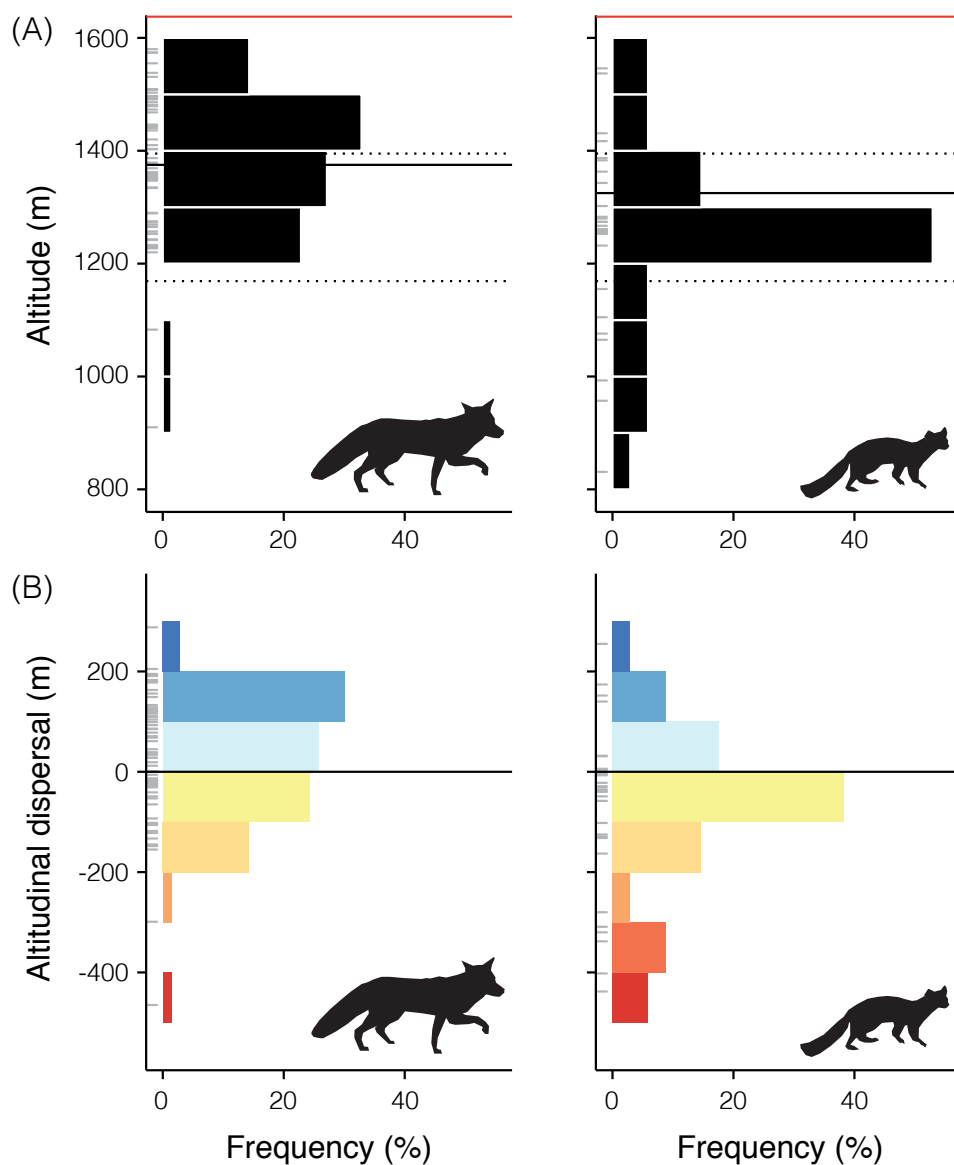


Figure 2. Relationships between horizontal (Euclidean) and altitudinal seed dispersal distances mediated by red foxes (circles, $n = 70$; solid line: $y = 25.7 + 0.064 x$) and pine martens (triangles, $n = 34$; dotted line: $y = -24.6 + 0.140 x$). As in Fig. 1B, the colour gradient is associated to 100-m altitudinal intervals in order to illustrate seed dispersal events towards colder and warmer ranges.

