

# 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 km<sup>2</sup>) 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  $\sim 70\text{-km}$  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 ( $^{18}\text{O}$  and  $^{16}\text{O}$ ) 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

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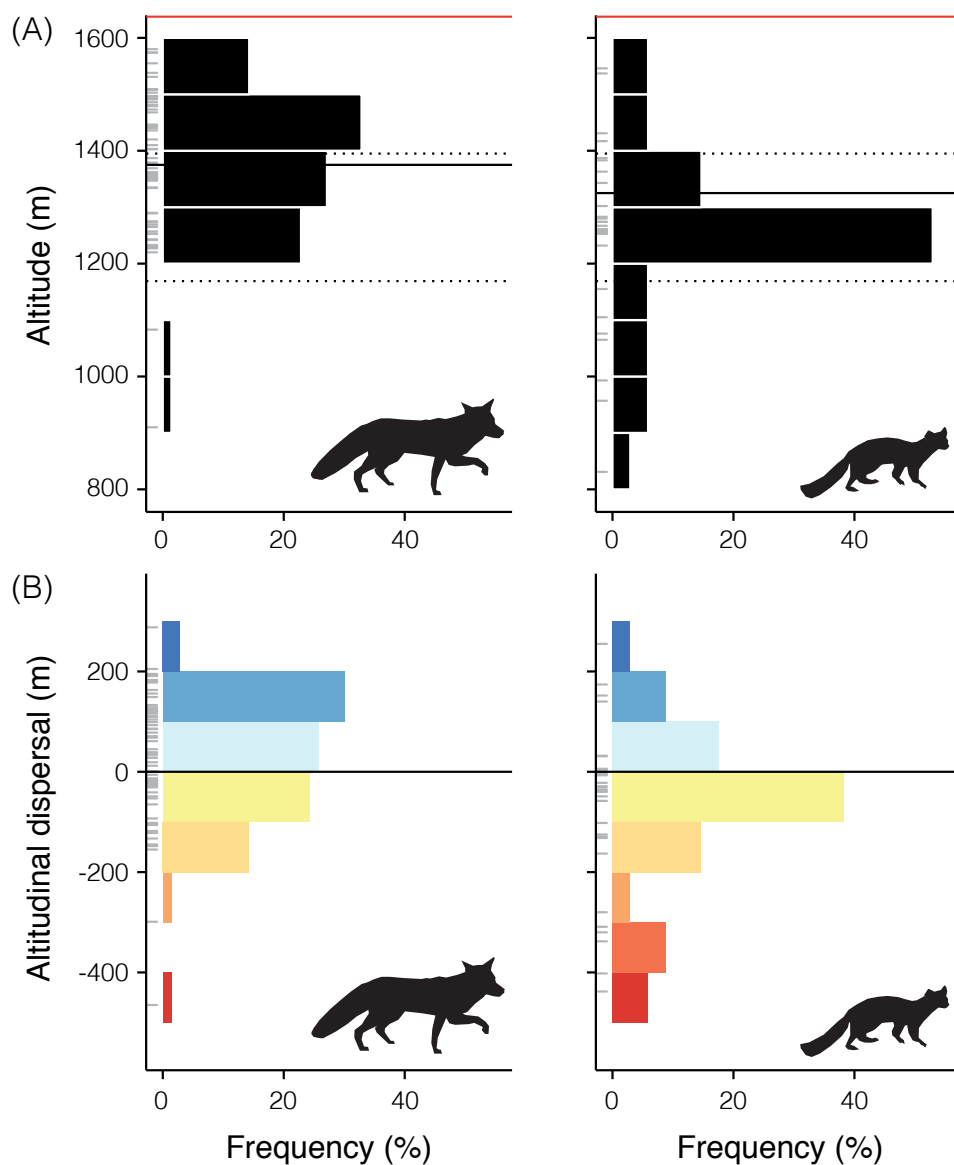
**Table 1.** Summary statistics of altitude of seed deposition and altitudinal seed dispersal distances mediated by red foxes and pine martens.

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 <sup>2</sup>	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  $\sim 1400$  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.

