

1 **Biotic interactions and seed deposition rather than abiotic factors determine**
2 **recruitment at elevational range limits of an alpine tree**

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17 Running headline: **Biotic factors and dispersal affect tree recruitment**

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19 **Summary**

20 1. Abiotic factors, biotic interactions and dispersal ability determine the spatial
21 distribution of species. Theory predicts that abiotic constraints set range limits under
22 harsh climatic conditions and biotic interactions set range limits under benign climatic
23 conditions, whereas dispersal ability should limit both ends of the distribution. However,
24 empirical studies exploring how these three components jointly affect species across
25 environmental gradients are scarce.

26 2. Here we present a study that jointly examines these factors to investigate the
27 constraints of the recruitment of Swiss stone pine (*Pinus cembra*) at and beyond its upper
28 and lower elevational range limits in the Swiss Alps. We investigated the natural
29 recruitment of pines and additionally conducted seed transplant experiments to test how
30 much abiotic factors (mean summer and winter temperatures, soil moisture), biotic
31 interactions (understorey vegetation cover, canopy cover, seed predation) and / or seed
32 deposition by the spotted nutcracker (*Nucifraga caryocatactes*) affect pine establishment.

33 3. We found significant effects of biotic interactions and seed deposition by spotted
34 nutcrackers on the recruitment of Swiss stone pine at both the upper and lower
35 elevational range, but could not detect significant effects of abiotic factors. Importantly,
36 dispersal limitation rather than temperature and soil moisture restricted the recruitment of
37 pines at the upper elevational range.

38 4. *Synthesis*. Our study highlights the importance of biotic interactions and dispersal
39 ability in setting the upper range limits of species that have been regarded as mainly
40 controlled by climate. This suggests that potential range shifts of plants in response to

41 climate warming may strongly depend on seed dispersal and biotic interactions and not
42 only on climatic factors.

43

44 Keywords: elevational gradient, *Nucifraga caryocatactes*, *Pinus cembra*, range shifts,
45 seed dispersal, transplant experiments

46 **Introduction**

47 Three important components have been distinguished to determine the geographic
48 distribution of species: local abiotic factors, biotic interactions and the ability of species
49 to disperse (e.g., Soberón 2007; Gaston 2009; Holt 2009). Theories that account for
50 environmental heterogeneity suggest that abiotic constraints primarily determine range
51 limits under harsh conditions (e.g., at high latitudes or elevations), and biotic interactions
52 mainly determine range limits under benign conditions (e.g., at low latitudes or
53 elevations; reviewed in Louthan et al. 2015), whereas dispersal limitation affects both
54 ends of species' distributions (Gaston 2009, Fig. 1). However, empirical evidence to
55 support these theories and explore how abiotic factors, biotic interactions and species'
56 dispersal ability jointly affect species across large environmental gradients is scarce. In
57 particular, quantification of the effects of biotic interactions and dispersal ability on
58 distributions is challenging and often limited by methodological constraints (Guisan &
59 Zimmermann 2000; Van der Putten, Macel & Visser 2010; HilleRisLambers *et al.* 2013).

60 Human-induced climate change globally modifies species' occurrences and is
61 predicted to intensify in the near future (Thomas *et al.* 2004; Pimm 2009). Already many
62 species have responded to climate warming by shifting their ranges towards higher
63 latitudes and elevations (Lenoir *et al.* 2008; Harsch *et al.* 2009; Chen *et al.* 2011; Zhu,
64 Woodall & Clark 2012). The degree of shifts in distribution is, however, very variable
65 among species. Until now, it is not clear to which extent climatic constraints, biotic
66 interactions or dispersal ability explain why some species adjust to climate change by
67 shifting their ranges and others do not (Thuiller 2004; Angert *et al.* 2011). Few studies go
68 beyond the comparison between current and previous range limits and empirically test the

69 mechanisms of range shifts. Several studies suggest that non-climatic factors, such as
70 biotic interactions or dispersal ability, could explain the variable responses of species to
71 changing climates (Zhu *et al.* 2012; HilleRisLambers *et al.* 2013). Modelling approaches
72 have attempted to incorporate biotic interactions (Guisan & Thuiller 2005; Meier *et al.*
73 2010; Puerta-Piñero, Pino & Gómez 2012) and dispersal ability (Westcott *et al.* 2005;
74 Russo, Portnoy & Augspurger 2006; Uriarte *et al.* 2011) in models of range dynamics
75 and have demonstrated their potential importance in shaping species' distributions.
76 Transplant experiments, especially of plants, comparing the fitness and survival ability of
77 the species within and beyond their ranges, have further been used to infer potential
78 dispersal limitation of species under the effects of changing climates (Hargreaves, Samis
79 & Eckert 2014; Dvorský *et al.* 2016). To better understand the mechanisms of range
80 dynamics in response to environmental change, simultaneous empirical testing of all
81 three components is necessary.

82 We present a study jointly investigating all three components. We examined how
83 abiotic factors, biotic interactions and dispersal ability determine the establishment of the
84 Swiss stone pine (*Pinus cembra* L.), a keystone tree species of subalpine forests of the
85 treeline ecotone. We investigated the establishment of Swiss stone pine along its
86 elevational distribution, because elevational gradients allow the study of broad
87 environmental conditions on rather small geographic scales (Popy, Bordignon & Prodon
88 2010). Swiss stone pine has its largest distribution in the central European Alps, where it
89 co-occurs with European larch (*Larix decidua* Mill.) and often forms the treeline. It
90 occurs across a short elevational gradient ranging from about 1500 – 2400 m a.s.l. (Ulber,
91 Gugerli & Bozic 2004). At its lower elevational range limit, it is outcompeted by other

92 tree species, in particular spruce [*Picea abies* (L.) H. Karst.]. The pine lives in close
93 interaction with its primary disperser, the spotted nutcracker [*Nucifraga caryocatactes*
94 (Linnaeus, 1758)], which is the only animal that may open the closed cones of the pine
95 and extract the seeds to store them in caches beneath the soil surface for later
96 consumption (Neuschulz *et al.* 2015). Hence, these birds are the only significant dispersal
97 vectors of Swiss stone pine. The global distribution of spotted nutcrackers is larger than
98 that of Swiss stone pine (Mattes *et al.* 1982), indicating that pine occurrence beyond its
99 distribution edges might not necessarily be restricted by the presence of its disperser. In
100 fact, distribution models of the tree species have suggested that Swiss stone pine is
101 strongly influenced by climatic factors rather than by biotic constraints (Meier *et al.*
102 2010).

103 In this study, we combined field observations of the natural recruitment of pines
104 and seed transplant experiments to investigate how abiotic factors (i.e., mean summer and
105 winter temperatures, soil moisture), biotic interactions (i.e., understorey vegetation cover,
106 canopy cover, rodent seed predation) and dispersal ability (i.e., seed deposition by spotted
107 nutcrackers) constrain the recruitment of Swiss stone pine. We show bird-mediated seed
108 deposition, which in the strict sense is a biotic interaction, separately from other biotic
109 interactions to better illustrate the three components determining species occurrence. We
110 tested how the three components affect pine recruitment and establishment across and
111 beyond its entire elevational range and separately at its lower and upper range limits. The
112 deposition of seeds by nutcrackers and the absence of other effective dispersal vectors,
113 such as wind, offers the unique opportunity to study the dispersal ability of an animal-
114 dispersed tree. We hypothesised that abiotic factors, such as temperature, would control

115 the occurrence of the pine at the upper elevational range where climatic conditions are
116 harsh (Vittoz *et al.* 2008; Meier *et al.* 2010; Boden, Pyttel & Eastaugh 2010), whereas
117 biotic controls, such as plant–plant interactions would affect the occurrence of the pine at
118 its lower elevational range where climatic conditions are benign (Ulber *et al.* 2004). We
119 expected little dispersal limitation at both ends of the pine’s range, due to the efficiency
120 and mobility of its seed disperser, the spotted nutcracker (Mattes 1982).

121

122 **Materials and methods**

123 *Study area and design*

124 The study was conducted within the core distribution of Swiss stone pine in the eastern
125 Swiss Alps, in the Canton of Grisons (Fig. S1). Field sites were located in two valleys
126 close to Davos, Flüela (46°48’0.25’’N, 9°54’15.38’’E) and Sertig (46°44’0.76’’N,
127 9°51’3.50’’E). In both valleys, Swiss stone pine forms the upper treeline and occurs at
128 elevations from about 1850 m to 2200 m a.s.l. Highest pine densities occur at
129 intermediate elevations within the elevational range. The treeline (upper elevational limit
130 at which trees reach three metres in height, Harsch *et al.* 2009) reaches 2150 m a.s.l., but
131 “krummholz” trees are found up to 2200 m a.s.l. The lower elevational range of Swiss
132 stone pine is dominated by spruce (*Picea abies*) forest.

133

134 *Abiotic factors, biotic interactions and seed deposition*

135 We tested the effect of 1) abiotic factors (i.e., mean summer and winter temperatures, soil
136 moisture), 2) biotic plant–plant and plant–animal interactions (i.e., understorey vegetation
137 cover, canopy cover, seed predation) and 3) dispersal ability (i.e., seed deposition by

138 spotted nutcrackers) that in previous publications have been studied in isolation and were
139 considered to be the most important factors for the regeneration of Swiss stone pine (e.g.,
140 Vittoz *et al.* 2008; Zurbriggen *et al.* 2013). We focused on the pine's early life stages, as
141 the ability of a plant to establish under new environmental conditions is key to respond to
142 potential climatic changes (Vitasse *et al.* 2012). 1) Abiotic factors: Low summer and
143 winter temperatures are restrictive for plant establishment and growth at the treeline,
144 restricting tissue formation of plants in the growing season (e.g., Rossi *et al.* 2007) and
145 causing plant mortality during winter (Vittoz *et al.* 2008). Soil water content is an
146 indicator for potential drought stress of plants (Anfodillo *et al.* 1998). Shallow and
147 permeable soils that frequently occur at high elevations often cause dry soil conditions
148 (Anfodillo *et al.* 1998), which can negatively affect seedling establishment (Moyes *et al.*
149 2012). 2) Biotic interactions: Understorey vegetation cover provides shelter for seedlings
150 and therefore is particularly important for plant establishment in harsh alpine
151 environments (Graae *et al.* 2011; Mamet & Kershaw 2013). In contrast, dense shrub
152 cover can also impair seedling growth, because of high interspecific competition (Liang
153 *et al.* 2016). Canopy cover determines the availability of light, which is essential for the
154 photosynthetic activity of plants. At the same time, elevated UV-B radiation, which is
155 particularly severe at sites with low canopy cover at high elevations, may negatively
156 affect seedling establishment processes (van de Staaij *et al.* 1997). Finally, the predation
157 of seeds, for instance by rodent seed predators, is an essential determinant of regeneration
158 across and beyond plant range limits that may strongly reduce seedling establishment
159 (e.g., Castro *et al.* 1999; Brown & Vellend 2014). 3) Dispersal ability: Many plants
160 depend on animals for the dispersal of their seeds. The dispersal and deposition of seeds

161 by spotted nutcrackers is of particular importance for the regeneration of Swiss stone pine,
162 as its cones, in adaptation to bird dispersal, remain closed on the tree until harvested by
163 the birds. Nutcrackers are the only animals that may open the cones and extract the seeds
164 with their strong bills (Mattes 1982). Therefore, Swiss stone pine strongly depends on
165 seed-caching nutcrackers for regeneration.

166

167 *Natural recruitment of Swiss stone pine*

168 We monitored the natural recruitment of Swiss stone pine seedlings and saplings across
169 and beyond its elevational distribution in both the Flüela and Sertig valleys in September
170 for three consecutive years, from 2012 to 2014. In each valley and year, we established 9
171 rectangular 20 m² plots at randomly selected locations between 1850 and 2250 m a.s.l.,
172 spaced by 50 m vertical height difference. Plots at 2250 m a.s.l. were established beyond
173 the upper range limit of Swiss stone pine. In each year, the 20-m² plots were placed at
174 different locations, resulting in 54 20-m² plots and a total area of 1080 m² sampled over
175 the three years. We recorded the total number of seedlings and saplings up to 1 m height
176 per plot. Due to the variable growth form of pine juveniles, it was not possible to classify
177 different age classes of seedlings and saplings in a non-destructive way.

178 To record the abiotic conditions, biotic interactions and seed deposition for each
179 20 m² plot, we divided each plot into 20 1-m² sub-plots. To obtain mean summer and
180 winter temperatures, we classified each sub-plot into one of the following four
181 microhabitat types: open soil, dwarf vegetation, rocky habitat, and close to tree trunk. We
182 measured temperature with 531 data loggers (Maxim iButton) that recorded soil surface
183 temperatures every four hours over the entire 3-year study period. Temperature data

184 loggers were equally distributed across all nine elevational bands (i.e., 1850 – 2250 m) in
185 both valleys, covering the four microhabitat types at each elevation. We calculated the
186 mean, minimum and maximum temperature of the warmest three months (June–August)
187 and the mean, minimum and maximum temperature of the coldest three months
188 (December–February) for each microhabitat type at each elevational band per valley over
189 the study period. We estimated the temperature for each of the 20 sub-plots based on its
190 microhabitat type, elevation, valley and year, and calculated average summer and winter
191 temperatures over all 20 sub-plots for each 20 m² plot. As minimum and maximum
192 temperatures were correlated to the mean of summer and winter temperatures, we did not
193 use these variables in the analyses. We also calculated growing degree-days (GDD)
194 according to the formula $GDD = [(T_{max} + T_{min}) / 2] - T_{base}$, where T_{max} / T_{min} are
195 daily maximum and minimum temperatures and T_{base} is the temperature below which
196 plant growth does not progress (McMaster & Wilhelm 1997). We set T_{base} to 5 °C
197 according to Körner & Paulsen (2004). Any daily minimum temperature below T_{base}
198 was set to T_{base} before calculating the average. Mean soil moisture per plot was recorded
199 by averaging measurements of soil moisture (in percent) over all 20 sub-plots. Soil
200 moisture measurements were taken each year in September under dry weather conditions
201 by averaging five tensiometer (Theta-Kit version 3) measurements, sampled within 5 cm
202 of the centre of each sub-plot.

203 Mean understorey vegetation cover per plot was recorded by averaging
204 measurements of dwarf shrub vegetation, such as European blueberry (*Vaccinium*
205 *myrtillus* L.), common juniper (*Juniperus communis* L.) and alpenrose (*Rhododendron*
206 *ferrugineum* L.), within each sub-plot according to Braun-Blanquet (1964). Mean canopy

207 cover per plot was recorded by averaging the canopy cover of each of the 20 sub-plots
208 sampled by a spherical crown densitometer (Forestry suppliers).

209 To obtain a comparable estimate of the number of seed caches deposited by
210 nutcrackers per 20 m² plot, we took 1-dm³ soil samples in the centre of each of the 20
211 sub-plots in which we thoroughly searched for seed caches established by the birds (i.e.,
212 1080 soil samples total over the three years, Briggs, Vander Wall & Jenkins 2009). A
213 previous study has shown that this method reveals the same patterns of seed deposition as
214 recorded by focal observations of seed-caching nutcrackers (Neuschulz *et al.* 2015). If an
215 intact seed or a seed shell handled by a nutcracker was present in the soil sample, we
216 recorded cache presence and later summed the overall number of caches per plot. As
217 nutcrackers are the main dispersal vector for Swiss stone pine seeds, the presence of
218 seeds in the soil is a clear indication for seed deposition by nutcrackers.

219

220 *Experimental seedling establishment*

221 To investigate the potential of pine seedling establishment across and beyond the current
222 elevational range of the pine, we conducted seed transplant experiments in the years 2012
223 and 2014. We deployed 90 experimental caches in each of the two valleys in May after
224 snowmelt, resulting in a total number of 360 experimental caches in both valleys over the
225 study period of two years. We chose the time after snowmelt, as this is the typical time
226 when Swiss stone pine seedlings start to germinate under natural conditions. At each of
227 the nine elevations, ranging from 1850 to 2250 m a.s.l., and spaced again by 50 m
228 vertical height difference, we deployed caches in five microhabitat types (open soil;
229 dwarf vegetation; rocky habitat; close to tree trunks; microsite covered by snow).

230 Experimental caches were placed close to, but not at the same sites as the 20 m² plots of
231 natural pine recruitment. Due to the absence of trees at high elevation plots (2250 m
232 a.s.l.), we exchanged the microhabitat “close to tree trunk” by sites in dense matgrass
233 cover (*Nardus stricta*). We intentionally followed this random-stratified design to
234 comprehensively cover the environmental space available at the selected mountain slopes.
235 Two replicates per microhabitat were established, resulting in 10 experimental caches at
236 each of the 9 elevations per year. Each cache contained five seeds (total number of seeds
237 over two years = 1800), placed 4 cm deep in the soil in a soil-filled mesh bag that was
238 open at the top and fixed by metal pins. We chose the number of five seeds as this was
239 the average number of seeds recorded for seed caches established by spotted nutcrackers
240 (Mattes 1982). Prior to the experiments, seeds had been treated to break dormancy (i.e.
241 stored in a moistened 1:1 clay–sand mixture under varying temperatures for 10 weeks),
242 which would naturally happen during winter time. Three months after planting, we
243 checked whether seedlings had established (germinated or established seedlings), seeds
244 had been predated or removed by rodents (gnawed or missing seeds), or seeds remained
245 intact.

246 At every experimental cache, we measured the mean summer temperature, GDD,
247 mean soil moisture, canopy cover and understory vegetation cover (methods described
248 in the section above). Mean temperature of the warmest three months of the growing
249 season (June–August) was recorded using 270 data loggers that were installed at
250 experimental caching sites and recorded soil surface temperatures every four hours. In
251 2012, data loggers were installed at one out of two experimental caches per microhabitat
252 at each elevation and valley, whereas in 2014 data loggers were installed at each

253 experimental cache. We also measured the proportions of ground-layer cover of grass,
254 pine needles, bare ground and nutrient availability at each experimental cache to capture
255 the fine-scale seedbed conditions. As grass and needle cover were significantly
256 negatively correlated to understorey dwarf shrub vegetation cover (grass cover: Pearson's
257 $r = -0.68$, $t = -6.76$, d.f. = 52, $p < 0.001$; needle cover: Pearson's $r = -0.50$, $t = -3.83$, d.f. =
258 52, $p < 0.001$), and bare ground and nutrient availability were significantly correlated to
259 soil moisture (bare ground: Pearson's $r = -0.34$, $t = -2.63$, d.f. = 52, $p = 0.011$; nutrient
260 availability: Pearson's $r = 0.60$, $t = 4.36$, d.f. = 52, $p < 0.001$), we did not use these
261 variables in the analyses.

262

263 *Data analyses*

264 First, we modelled natural pine recruitment (i.e., number of juvenile plants per plot) and
265 experimental seedling establishment (i.e., probability of seedlings to establish from all
266 sown seeds) as a function of elevation using generalized linear models (GLMs). We
267 modelled natural pine recruitment assuming a quasi-Poisson error distribution accounting
268 for overdispersion and experimental seedling establishment assuming a binomial error
269 distribution. Both models included a quadratic and linear term of elevation as fixed
270 effects and the valley and the study year as fixed effect control variables. We selected the
271 best model based on Akaike's information criterion for small sample size (AICc, Hurvich
272 and Tsai 1989) and its equivalent for overdispersed models (qAICc, Bartón 2015). In the
273 model of natural pine recruitment, we retained a linear and a quadratic term of elevation
274 and in the model of experimental seedling establishment, we retained a linear term of
275 elevation.

276 Second, we modelled each abiotic factor, biotic interaction and seed deposition
277 measured in the recordings of natural and experimental pine recruitment as a function of
278 elevation using GLMs. All models also included the valley and the study year as fixed
279 effect control variables. Mean summer and winter temperatures were modelled assuming
280 a normal distribution. Soil moisture, understorey vegetation cover, canopy cover, and
281 seed predation (i.e., proportion of predated seeds per cache) were modelled assuming a
282 quasi-binomial error distribution accounting for overdispersion. Seed deposition (i.e.,
283 number of seed caches) was modelled assuming a quasi-Poisson error distribution
284 accounting for overdispersion. In all models, we fitted a quadratic and linear term of
285 elevation and selected the best model based on Akaike's information criterion for small
286 sample size (AICc, Hurvich and Tsai 1989) and its equivalent for overdispersed models
287 (qAICc, Bartón 2015). We retained both the quadratic and linear term of elevation in all
288 models, except in the models of mean summer temperature and seed predation in which
289 only the linear term of elevation was retained.

290 Third, we tested the importance of all abiotic factors, biotic interactions and seed
291 deposition as predictors for natural pine recruitment and experimental seedling
292 establishment across and beyond the entire elevational range of Swiss stone pine (1850 m
293 – 2250 m a.s.l.). To quantify and compare the predictor's importance at the lower and
294 upper range limit of the species, we also separately analysed the lower range (< 2050 m
295 a.s.l., four elevational bands) and upper range (> 2050 m a.s.l., four elevational bands).
296 Prior to these analyses, we tested for collinearity of the predictor variables. As
297 understorey vegetation cover was significantly negatively correlated with canopy cover
298 (natural pine recruitment: Pearson's $r = -0.50$, $t = -4.06$, d.f. = 49, $p < 0.001$; transplant

299 experiments: Pearson's $r = -0.46$, $t = -9.69$, d.f. = 343, $p < 0.001$), we excluded canopy
300 cover from the final analyses. We also excluded GDD from the final analyses due to
301 significant positive correlation to mean summer temperature (natural pine recruitment:
302 Pearson's $r = 0.71$, $t = 7.20$, d.f. = 52, $p < 0.001$). However, we additionally present
303 models including canopy cover (instead of understorey vegetation cover) and GDD
304 (instead of mean summer and winter temperatures) in the Appendix. To provide
305 comparability of the predictor estimates among each other, all predictor variables were
306 centred and standardized using Gelman's approach prior to the analysis using the *arm*
307 package (Grueber *et al.* 2011; Gelman 2016). We fitted full GLMs including all
308 combinations of the predictor variables of the models using the *MuMIn* package (Bartón
309 2015). Models of natural pine recruitment included mean summer temperature, mean
310 winter temperature and soil moisture, understorey vegetation cover (canopy cover,
311 respectively), and the number of caches and were modelled assuming a quasi-Poisson
312 error distribution accounting for overdispersion. Models of experimental seedling
313 establishment included mean summer temperature, soil moisture, seed predation, and
314 understorey vegetation cover (canopy cover, respectively) and were modelled using a
315 quasi-binomial error distribution accounting for overdispersion. All models also included
316 the valley and the study year as fixed effect control variables. First, we obtained the
317 relative importance of each predictor variable in the full models. We conducted model
318 averaging by using the standardized regression coefficients of all candidate models
319 weighted by the model's $qAICc$ weights. The variable importance values of all predictor
320 variables were then scaled to sum up to one for comparison between models of natural
321 pine recruitment and experimental seedling establishment. Second, we selected the best

322 models based on $\Delta qAICc < 5$ and calculated model estimates based on model averaging
323 of these best models (Bartón 2015).

324

325 **Results**

326 *Natural and experimental recruitment of Swiss stone pine across the elevational gradient*

327 We recorded 135 pine seedlings and saplings in 54 20-m² plots across the elevational
328 gradient in both valleys and all years. The natural recruitment of pines showed a hump-
329 shaped distribution with the highest predicted number of four juveniles per 20-m² plot at
330 2070 m a. s. l. averaged across both valleys (Fig. 2a).

331 In the transplant experiments, 193 seedlings established out of 1800 seeds planted
332 over two years. Unlike the natural recruitment of pines, seedling establishment in the
333 transplant experiments increased with increasing elevation (Fig. 2b). While the predicted
334 probability of seedling establishment was only 3 % at the lower edge of the elevational
335 range at 1850 m a.s.l., the probability of seedling establishment was 17 % beyond the
336 current distribution of the pine at 2250 m a.s.l.

337

338 *Abiotic factors, biotic interactions and seed deposition across the elevational gradient*

339 Patterns of abiotic factors, biotic interactions, and seed deposition measured at both
340 observational plots and experimental sites significantly differed across the elevational
341 gradient (Figs 3 and S2, Tables S1 and S2). Mean summer temperature significantly
342 increased with increasing elevation, reflecting the high solar radiation that seedlings
343 experience in summer at high elevations, which was measured by the temperature loggers
344 at the soil surface (Figs 3a and S2a, Tables S1 and S2). Mean winter temperature showed

345 a slight, but non-significant decrease across the elevational gradient (Fig. 3b, Tables S1).
346 Soil moisture showed a u-shaped distribution across the elevational gradient, with lowest
347 values at mid-elevations (Figs 3c and S2b, Tables S1 and S2). While canopy cover
348 significantly decreased across the elevational gradient (Fig. S2c, Tables S1 and S2),
349 understorey vegetation cover significantly increased with elevation (Figs 3d and S2d,
350 Tables S1 and S2). Out of 1800 seeds planted in the transplant experiments over two
351 years, 764 seeds were preyed upon or removed by rodents. Seed predation was high at
352 low elevations (predicted probability of 74 % at 1850 m a.s.l.) and significantly declined
353 across the elevational gradient (predicted probability of 28 % at 2250 m a.s.l., Fig. 3e,
354 Table S2). In 152 out of 1080 soil samples, we recorded seed caches deposited by spotted
355 nutcrackers. Seed deposition followed a hump-shaped distribution, with the highest
356 predicted number of 4.9 caches per plot at 2025 m a.s.l. averaged across all valleys and
357 years (Fig. 3f, Tables S1).

358

359 *Relative importance of abiotic factors, biotic interactions, and seed deposition for*
360 *natural and experimental pine recruitment*

361 Seed deposition and biotic interactions explained more than half of the relative
362 importance of factors affecting the natural recruitment of pines and experimental seedling
363 establishment across and beyond the elevational range of the tree (Fig. 4). Abiotic factors
364 contributed with a relative importance of 0.23 in explaining the natural recruitment of
365 pines across elevations. In contrast, understorey vegetation cover and seed deposition
366 together had a relative importance of 0.72 (Fig. 4a). A similar pattern was found in the
367 transplant experiments where abiotic factors contributed with a relative importance of

368 0.13 in explaining experimental seedling establishment. In contrast, understorey
369 vegetation cover and seed predation together had a relative importance of 0.86 (Fig. 4b).
370 At the upper range of the distribution of Swiss stone pine, the relative importance of
371 abiotic factors was 0.16 in explaining natural pine recruitment and 0.10 in explaining
372 experimental seedling establishment, whereas the relative importance of seed deposition
373 and biotic interactions was 0.67 for natural pine recruitment and 0.83 for experimental
374 seedling establishment (Fig. 4a, b “Upper range”). At the lower range of the distribution
375 of Swiss stone pine, the relative importance of abiotic factors was 0.42 in explaining
376 natural pine recruitment and 0.07 in explaining experimental seedling establishment,
377 whereas the relative importance of seed deposition and biotic interactions was 0.06 for
378 natural pine recruitment and 0.89 for experimental seedling establishment (Fig. 4a, b
379 “Lower range”). All models using canopy cover instead of understorey vegetation cover
380 showed qualitatively similar results (Fig. S3). This pattern was confirmed by qAIC-based
381 model selection, showing significant effects for understorey vegetation cover, canopy
382 cover, seed predation and seed deposition on natural pine recruitment and experimental
383 seedling establishment (Table 1, Table S3). Abiotic factors were not significant in all the
384 best models of Swiss stone pine recruitment (Table 1, Table S3).

385

386 **Discussion**

387 To date, there is little empirical evidence of how abiotic factors, biotic interactions, and
388 dispersal ability jointly determine range limits of plants (but see Puerta-Piñero *et al.*
389 2012; Brown & Vellend 2014). Many previous studies have attributed range limits
390 especially in harsh environments to abiotic conditions (e.g., Normand *et al.* 2009; Lee-

391 Yaw *et al.* 2016) and projections of potential range shifts under climate change are often
392 solely based on abiotic factors (e.g., Shevtsova *et al.* 2009; Engler *et al.* 2011). We here
393 provide a comprehensive study on species range limits that includes all three components.
394 We find evidence that seed deposition and biotic interactions determined the recruitment
395 of Swiss stone pine and not, as expected, harsh abiotic conditions at the upper range limit
396 (Vittoz *et al.* 2008; Boden *et al.* 2010). Transplant experiments demonstrated that
397 seedlings could establish above the current tree line. However, patterns of seed deposition
398 by nutcrackers suggested that dispersal to high elevations might be rare and seeds do not
399 frequently reach locations beyond the treeline. Our findings demonstrate that
400 understanding the underlying mechanisms of dispersal ability and biotic interactions is,
401 beside the consideration of abiotic factors, important for projecting potential range shifts
402 of plants under climate change.

403 Spotted nutcrackers cached seeds primarily within the range limits of the current
404 elevational distribution of the pine, which appeared to be the main factor restricting the
405 elevational range of the tree species. These findings were supported by the high
406 probability of pine seedling establishment beyond the treeline in the transplant
407 experiments, indicating potential dispersal limitation of the tree. Our results were
408 surprising, as plants growing at steep elevational gradients are generally not regarded as
409 dispersal limited because of the small spatial extent of a large variety of different habitats
410 (Jump, Mátyás & Peñuelas 2009; Hargreaves *et al.* 2014; Siefert, Lesser & Fridley 2015).
411 Spotted nutcrackers are able to conduct far-ranging seed dispersal flights among valleys
412 (Mattes 1982) and their high mobility should not restrict pine seed dispersal. Several
413 reasons could explain the low seed deposition beyond the current limits of pine

414 distribution: Spotted nutcrackers prefer microsites for seed caching where the
415 perishability of stored seeds is low, hence the probability of seedling establishment is low
416 (Neuschulz *et al.* 2015). Nutcrackers thus might avoid caching seeds beyond the treeline
417 as these seeds have a high probability of establishment, which would spoil them as a
418 potential food source. Also, the lack of landmarks such as trees beyond the treeline
419 (Smulders, Gould & Leaver 2010) and the very deep snow at high elevation sites during
420 winter (Mattes 1982) could hinder the recovery of seed caches by the birds. Despite the
421 low seed deposition at high elevations, juvenile pines occurred in our study area at
422 elevations up to 2200 m a.s.l. An explanation for this high elevation occurrence could be
423 the synchronous production of above-average seed-crops every few years, which is
424 typical for Swiss stone pine (Zong *et al.* 2010), but which we did not encounter in our
425 study period. Animals have been shown to disperse seeds in mast years more frequently
426 and farther compared to typical seed-production years (Vander Wall 2002). While the
427 probability of seed deposition beyond the treeline averaged over several years might be
428 low, nutcrackers might expand their caching sites to high elevations in mast seeding years.
429 In summary, our results underpin that potential upwards movements of the Swiss stone
430 pine under climate warming may strongly depend on the caching behaviour of its main
431 disperser, the spotted nutcracker. While the close mutualistic interaction between
432 nutcracker and pine gave us the unique opportunity to study the dispersal ability of the
433 tree species in great detail, we are aware that the prominent role of seed deposition by
434 spotted nutcrackers for pine establishment might be specific for this highly specialized
435 plant–bird system. However, previous studies that have investigated the often neglected
436 spatially-explicit patterns of seed deposition across heterogeneous environments show the

437 effects of distinct and non-random deposition of seeds by different dispersal vectors, such
438 as wind or animals (e.g., Gómez-Aparicio, Gomez & Zamora 2007; Damschen *et al.*
439 2014; Mueller *et al.* 2014). We therefore believe that seed deposition might be more
440 important for local range expansions than previously assumed.

441 Interestingly, not only seed deposition, but also biotic interactions (i.e.,
442 understorey vegetation and the lack of seed predation) influenced Swiss stone pine
443 establishment at the upper range of the species more than abiotic factors, which contrasts
444 the long-standing prediction that climate sets the range limits in abiotically stressful
445 environments (e.g., reviewed in Louthan *et al.* 2015, Fig. 1). Recent studies provide
446 increasing evidence that biotic interactions are often equally important as abiotic factors
447 for plant establishment at high elevations (HilleRisLambers *et al.* 2013; Brown &
448 Vellend 2014; Tingstad *et al.* 2015; Liang *et al.* 2016). Dense shrub cover has, for
449 instance, been shown to reduce seedling establishment at treeline ecotones (Tingstad *et*
450 *al.* 2015) and thus, may decelerate the potential upwards movements of tree species under
451 climate change (Liang *et al.* 2016). In our study, understorey vegetation cover fostered
452 the natural recruitment and experimental establishment of Swiss stone pine. Plants
453 growing in stress-prone environments often experience ameliorated microhabitat
454 conditions in dense shrub vegetation (e.g., Callaway *et al.* 2002; Gómez-Aparicio *et al.*
455 2004), such as beneficial soil conditions (HilleRisLambers *et al.* 2013), shelter and higher
456 humidity (Graae *et al.* 2011) or reduced herbivory (Cairns & Moen 2004). Seed predation
457 by rodents strongly reduced the establishment of pine seedlings. Similar patterns have
458 been shown by Brown and Vellend (2014) who found that high rates of rodent predation
459 on seeds of sugar maple (*Acer saccharum*) prevented the potential upward movement of

460 the tree species. In contrast to their findings, we found that seed predation was much
461 higher (over 70 %) at the lower range edge of Swiss stone pine compared to that beyond
462 the treeline (30 %), likely due to lower rodent densities at high elevations (McCain 2005).
463 Our results emphasise that biotic interactions play a crucial role in determining the
464 occurrence of plants across environmental gradients.

465 Temperature has widely been considered to control plant distribution limits (e.g.,
466 Normand *et al.* 2009; Vitasse *et al.* 2012; Louthan *et al.* 2015). While many studies have
467 shown that summer temperatures determine the formation of altitudinal and latitudinal
468 treelines (Körner & Paulsen 2004; Holtmeier & Broll 2007; Siefert *et al.* 2015), there is
469 also evidence that winter temperatures are decisive for treeline formation (e.g.,
470 Rickebusch *et al.* 2007; Harsch *et al.* 2009). Although the natural climatic treeline in the
471 Alps has been shifted downslope due to long-lasting anthropogenic disturbances (Gehrig-
472 Fasel, Guisan & Zimmermann 2007; Holtmeier & Broll 2007), climatic controls of plant
473 establishment and growth prevail (Holtmeier & Broll 2007; Vitasse *et al.* 2012). For
474 instance, seedlings of Swiss stone pine have been reported to suffer in particular from
475 extreme frost events (Barbeito *et al.* 2012) whereas long and cold winters may cause
476 severe growth depression and damage of juvenile and adult trees (Vittoz *et al.* 2008). In
477 our study, we did not find a significant effect of mean summer and winter temperatures
478 on the natural recruitment and experimental seedling establishment of Swiss stone pine,
479 neither across the entire elevational range nor at the upper range of the species. Although
480 winter temperature had a rather large relative importance in some of the models
481 explaining the natural recruitment of pines, its effects were not significant (Table S1). We
482 might have underestimated the effect of winter temperatures in our relatively short three-

483 year study, because cold winter events that could potentially affect pine populations in
484 the study area take place roughly every 4-5 years (Beniston 2012). Long-term studies of
485 climate effects on the establishment and survival of plants should be the focus of future
486 studies (Dvorský *et al.* 2016). Climate manipulation experiments in the field could further
487 be used to simulate the long-term effects of climate warming on seedling establishment
488 (De Boeck *et al.* 2015; Elmendorf *et al.* 2015). Yet, our study emphasises that in the
489 short-term, seed deposition by spotted nutcrackers and biotic interactions appear to
490 control the establishment and survival of Swiss stone pine across and beyond its upper
491 distribution limit.

492

493 **Conclusion**

494 Explaining the distribution of plants across environmental gradients has been a great
495 challenge in past research. Here we show that seed deposition and biotic interactions
496 determine the recruitment of an alpine tree species, the Swiss stone pine. Our findings
497 suggest that dispersal ability and biotic interactions may be dominant factors affecting the
498 early stages of the plant life cycle, particularly if plants depend on animal dispersal. This
499 has important implications for understanding species range dynamics along
500 environmental gradients, revealing that biotic interactions and dispersal ability are, beside
501 the already known abiotic factors, also important for explaining the occurrence of plants.
502 Our findings may not only apply to elevational, but also to latitudinal range limits of
503 plants. We expect that especially dispersal ability might control the occurrence of plants
504 at their latitudinal limits, because dispersal limitation has been shown to be even more
505 restrictive for plant range expansion at latitudinal than at elevational range edges (Siefert

506 *et al.* 2015). We believe that our findings have key implications for understanding the
507 range dynamics of plants growing along environmental gradients, emphasising that seed
508 deposition might be more important for local range expansions than previously assumed.

509

510 **Authors Contribution**

511 E.L.N. and K.G.B. conceived the ideas and designed methodology. E.L.N. and D.M.
512 collected the data. E.L.N. analysed the data and led the writing of the manuscript. E.L.N.,
513 D.M., K.B., F.G. and K.G.B. contributed to the various drafts and gave final approval for
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527

528 **Data accessibility**

529 Data from this paper are deposited in the Dryad Digital Repository
530 doi:10.5061/dryad.8t2q2 (Neuschulz *et al.* 2017).

531 **References**

- 532 Anfodillo, T., Rento, S., Carraro, V., Furlanetto, L., Urbinati, C. & Carrer, M. (1998)
533 Tree water relations and climatic variations at the alpine timberline: seasonal
534 changes of sap flux and xylem water potential in *Larix decidua*. *Annals of Forest*
535 *Science*, **55**, 159–172.
- 536 Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J.
537 (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology*
538 *Letters*, **14**, 677–89.
- 539 Barbeito, I., Dawes, M. A., Rixen, C., Senn, J. & Bebi, P. (2012) Factors driving
540 mortality and growth at treeline: a 30-year experiment of 92 000 conifers. *Ecology*,
541 **93**, 389–401.
- 542 Bartón, K. (2015) Multi-model inference: Package “MuMIn”. [https://cran.r-](https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf)
543 [project.org/web/packages/MuMIn/MuMIn.pdf](https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf)
- 544 Beniston, M. (2012) Is snow in the Alps receding or disappearing? *Wiley*
545 *Interdisciplinary Reviews*, **3**, 349–358.
- 546 Boden, S., Pyttel, P. & Eastaugh, C. (2010) Impacts of climate change on the
547 establishment, distribution, growth and mortality of Swiss stone pine (*Pinus cembra*).
548 *iForest - Biogeosciences and Forestry*, **3**, 82–85.
- 549 De Boeck, H. J., Vicca, S., Roy, J., Nijs, I., Milcu, A., Kreyling, J., Jentsch, A., Chabbi,
550 A., Campioli, M., Callaghan, T., Beierkuhnlein, C. & Beier, C. (2015) Global
551 change experiments: Challenges and opportunities. *BioScience*, **65**, 922–931.
- 552 Braun-Blanquet, J. (1964) *Pflanzensoziologie, Gundzüge der Vegetationskunde* (3rd Ed.).

553 Springer, Wien.

554 Briggs, J.S., Vander Wall, S.B. & Jenkins, S.H. (2009) Forest rodents provide directed
555 dispersal of Jeffrey pine seeds. *Ecology*, **90**, 675–87.

556 Brown, C.D. & Vellend, M. (2014) Non-climatic constraints on upper elevational plant
557 range expansion under climate change. *Proceedings of the Royal Society B*, **281**,
558 20141779.

559 Cairns, D.M. & Moen, J. (2004) Herbivory influences tree lines. *Journal of Ecology*, **92**,
560 1019–1024.

561 Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R.,
562 Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D.
563 & Cook, B.J. (2002) Positive interactions among alpine plants increase with stress.
564 *Nature*, **417**, 844–848.

565 Castro, J., Gómez, J.M., García, D., Zamora, R. & Hódar, J.A. (1999) Seed predation and
566 dispersal in relict Scots pine forests in southern Spain. *Plant Ecology*, **145**, 115–123.

567 Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range
568 shifts of species associated with high levels of climate warming. *Science*, **333**,
569 1024–1026.

570 Damschen, E.I., Baker, D. V, Bohrer, G., Nathan, R., Orrock, J.L., Turner, J.R., Brudvig,
571 L. A., Haddad, N.M., Levey, D.J. & Tewksbury, J.J. (2014) How fragmentation and
572 corridors affect wind dynamics and seed dispersal in open habitats. *Proceedings of*
573 *the National Academy of Sciences of the United States of America*, **111**, 3484–3489.

574 Dvorský, M., Chlumská, Z., Altman, J., Čapková, K., Řeháková, K., Macek, M.,

575 Kopecký, M., Liancourt, P. & Doležal, J. (2016) Gardening in the zone of death: an
576 experimental assessment of the absolute elevation limit of vascular plants. *Scientific*
577 *Reports*, **6**, 24440.

578 Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Fosaa, A. M., Gould, W. A.,
579 Hermanutz, L., Hofgaard, A., Jónsdóttir, I. I., Jorgenson, J. C., Lévesque, E.,
580 Magnusson, B., Molau, U., Myers-Smith, I. H., Oberbauer, S. F., Rixen, C.,
581 Tweedie, C. E. & Walker, M. D. (2015) Corrections for Elmendorf et al.,
582 Experiment, monitoring, and gradient methods used to infer climate change effects
583 on plant communities yield consistent patterns. *Proceedings of the National*
584 *Academy of Sciences*, **112**, E4156–E4156.

585 Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araújo, M.B.,
586 Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De
587 Lamo, X., Dirnböck, T., Gégout, J.-C., Gómez-García, D., Grytnes, J.-A., Heegaard,
588 E., Høistad, F., Nogués-Bravo, D., Normand, S., Puşcaş, M., Sebastià, M.-T.,
589 Stanisci, A., Theurillat, J.-P., Trivedi, M.R., Vittoz, P. & Guisan, A. (2011) 21st
590 century climate change threatens mountain flora unequally across Europe. *Global*
591 *Change Biology*, **17**, 2330–2341.

592 Gaston, K.J. (2009) Geographic range limits: achieving synthesis. *Proceedings of the*
593 *Royal Society B*, **276**, 1395–1406.

594 Gehrig-Fasel, J., Guisan, A. & Zimmermann, N. (2007) Tree line shifts in the Swiss
595 Alps: Climate change or land abandonment? *Journal of Vegetation Science*, **18**,
596 571–782.

597 Gelman, A. (2016) Data analysis using regression and multilevel/hierarchical models:

598 Package “arm”. <https://cran.r-project.org/web/packages/arm/arm.pdf>

599 Gómez-Aparicio, L., Gomez, J.M. & Zamora, R. (2007) Spatiotemporal patterns of seed
600 dispersal in a wind-dispersed Mediterranean tree (*Acer opalus* subsp. *granatense*):
601 Implications for regeneration. *Ecography*, **30**, 13–22.

602 Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J. & Baraza, E.
603 (2004) Applying plant facilitation to forest restoration: A meta-analysis of the use of
604 shrubs as nurse plants. *Ecological Applications*, **14**, 1128–1138.

605 Graae, B.J., Ejrnæs, R., Lang, S.I., Meineri, E., Ibarra, P.T. & Bruun, H.H. (2011) Strong
606 microsite control of seedling recruitment in tundra. *Oecologia*, **166**, 565–76.

607 Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011) Multimodel inference
608 in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology*,
609 **24**, 699–711.

610 Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than
611 simple habitat models. *Ecology Letters*, **8**, 993–1009.

612 Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology.
613 *Ecological Modelling*, **135**, 147–186.

614 Hargreaves, A.L., Samis, K.E. & Eckert, C.G. (2014) Are species’ range limits simply
615 niche limits writ large? A review of transplant experiments beyond the range.
616 *American Naturalist*, **183**, 157–173.

617 Harsch, M. A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009) Are treelines
618 advancing? A global meta-analysis of treeline response to climate warming. *Ecology*
619 *Letters*, **12**, 1040–1049.

- 620 HilleRisLambers, J., Harsch, M.A., Ettinger, A.K., Ford, K.R. & Theobald, E.J. (2013)
621 How will biotic interactions influence climate change-induced range shifts? *Annals*
622 *of the New York Academy of Sciences*, **1297**, 112–125.
- 623 Holt, R.D. (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and
624 evolutionary perspectives. *Proceedings of the National Academy of Sciences of the*
625 *United States of America*, **106**, 19659–19665.
- 626 Holtmeier, F.K. & Broll, G. (2007) Treeline advance - driving processes and adverse
627 factors. *Landscape Online*, **1**, 1–33.
- 628 Hurvich, C. & Tsai, C.-L. (1989) Regression and time series model selection in small
629 samples. *Biometrika*, **76**, 297–307.
- 630 Jump, A.S., Mátyás, C. & Peñuelas, J. (2009) The altitude-for-latitude disparity in the
631 range retractions of woody species. *Trends in Ecology and Evolution*, **24**, 694–701.
- 632 Körner, C. & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures.
633 *Journal of Biogeography*, **31**, 713–732.
- 634 Lee-Yaw, J.A., Kharouba, H.M., Bontrager, M., Mahony, C., Csörgő, A.M., Noreen,
635 A.M.E., Li, Q., Schuster, R. & Angert, A.L. (2016) A synthesis of transplant
636 experiments and ecological niche models suggests that range limits are often niche
637 limits. *Ecology Letters*, **19**, 710–722.
- 638 Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. (2008) A significant
639 upward shift in plant species optimum elevation during the 20th century. *Science*,
640 **320**, 1768–1771.
- 641 Liang, E., Wang, Y., Piao, S., Lu, X., Camarero, J.J., Zhu, H., Zhu, L., Ellison, A. M.,

642 Ciais, P. & Peñuelas, J. (2016) Species interactions slow warming-induced upward
643 shifts of treelines on the Tibetan Plateau. *Proceedings of the National Academy of*
644 *Sciences of the United States of America*, **113**, 4380–4385.

645 Louthan, A.M., Doak, D.F. & Angert, A.L. (2015) Where and when do species
646 interactions set range limits? *Trends in Ecology & Evolution*, **30**, 780–792.

647 Mamet, S.D. & Kershaw, G.P. (2013) Multi-scale analysis of environmental conditions
648 and conifer seedling distribution across the treeline ecotone of northern Manitoba,
649 Canada. *Ecosystems*, **16**, 295–309.

650 Mattes, H. (1982) *Die Lebensgemeinschaft von Tannenhäher Und Arve*. Berichte
651 Eidgenössische Anstalt für das forstliche Versuchswesen Nr. 241. Birmensdorf.

652 McCain, C.M. (2005) Elevational gradients in diversity of small mammals. *Ecology*, **86**,
653 366–372.

654 McMaster, G. S. & Wilhelm, W.W. (1997) Growing degree-days: one equation, two
655 interpretations. *Agricultural and Forest Meteorology*, **87**, 291–300.

656 Meier, E.S., Kienast, F., Pearman, P.B., Svenning, J.C., Thuiller, W., Araújo, M.B.,
657 Guisan, A. & Zimmermann, N.E. (2010) Biotic and abiotic variables show little
658 redundancy in explaining tree species distributions. *Ecography*, **33**, 1038–1048.

659 Moyes, A.B., Castanha, C., Germino, M.J. & Kueppers, L.M. (2012) Warming and the
660 dependence of limber pine (*Pinus flexilis*) establishment on summer soil moisture
661 within and above its current elevation range. *Oecologia*, **171**, 271–282.

662 Mueller, T., Lenz, J., Caprano, T., Fiedler, W. & Böhning-Gaese, K. (2014) Large
663 frugivorous birds facilitate functional connectivity of fragmented landscapes.

664 *Journal of Applied Ecology*, **51**, 684–692.

665 Neuschulz, E.L., Mueller, T., Bollmann, K., Gugerli, F. & Böhning-Gaese, K. (2015)

666 Seed perishability determines the caching behaviour of a food-hoarding bird.

667 *Journal of Animal Ecology*, **84**, 71–78.

668 Neuschulz, E.L., Merges, D., Bollmann, K., Gugerli, F. & Böhning-Gaese, K. (2017)

669 Data from: Biotic interactions and seed deposition rather than abiotic factors

670 determine recruitment at elevational range limits of an alpine tree. *Journal of*

671 *Ecology*, doi:10.5061/dryad.8t2q2

672 Normand, S., Treier, U.A., Randin, C., Vittoz, P., Guisan, A. & Svenning, J.-C. (2009)

673 Importance of abiotic stress as a range-limit determinant for European plants:

674 insights from species responses to climatic gradients. *Global Ecology and*

675 *Biogeography*, **18**, 437–449.

676 Pimm, S.L. (2009) Climate disruption and biodiversity. *Current Biology*, **19**, 595–601.

677 Popy, S., Bordignon, L. & Prodon, R. (2010) A weak upward elevational shift in the

678 distributions of breeding birds in the Italian Alps. *Journal of Biogeography*, **37**, 57–

679 67.

680 Puerta-Piñero, C., Pino, J. & Gómez, J.M. (2012) Direct and indirect landscape effects on

681 *Quercus ilex* regeneration in heterogeneous environments. *Oecologia*, **170**, 1009–

682 1020.

683 Van der Putten, W.H., Macel, M. & Visser, M.E. (2010) Predicting species distribution

684 and abundance responses to climate change: why it is essential to include biotic

685 interactions across trophic levels. *Philosophical Transactions of the Royal Society*

686 *B: Biological Sciences*, **365**, 2025–2034.

687 Rickebusch, S., Lischke, H., Bugmann, H., Guisan, A. & Zimmermann, N.E. (2007)

688 Understanding the low-temperature limitations to forest growth through calibration

689 of a forest dynamics model with tree-ring data. *Forest Ecology and Management*,

690 **246**, 251–263.

691 Rossi, S., Deslauriers, A., Anfodillo, T. & Carraro, V. (2007) Evidence of threshold

692 temperatures for xylogenesis in conifers at high altitudes. *Oecologia*, **152**, 1–12.

693 Russo, E.S., Portnoy, S. & Augspurger, C.K. (2006) Incorporating animal behavior into

694 seed dispersal models : Implications for seed shadows. *Ecology*, **87**, 3160–3174.

695 Shevtsova, A., Graae, B.J., Jochum, T., Milbau, A., Kockelbergh, F., Beyens, L. & Nijs, I.

696 (2009) Critical periods for impact of climate warming on early seedling

697 establishment in subarctic tundra. *Global Change Biology*, **15**, 2662–2680.

698 Siefert, A., Lesser, M.R. & Fridley, J.D. (2015) How do climate and dispersal traits limit

699 ranges of tree species along latitudinal and elevational gradients? *Global Ecology*

700 *and Biogeography*, **24**, 581–593.

701 Smulders, T. V, Gould, K.L. & Leaver, L.A. (2010) Using ecology to guide the study of

702 cognitive and neural mechanisms of different aspects of spatial memory in food-

703 hoarding animals. *Philosophical Transactions of the Royal Society B, Biological*

704 *Sciences*, **365**, 883–900.

705 Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of

706 species. *Ecology Letters*, **10**, 1115–1123.

707 Van de Staaij, J.W.M., Bolink, E., Rozema, J. & Ernst, W.H.O. (1997) The impact of

708 elevated UV-B (280 – 320 nm) radiation levels on the reproduction biology of a
709 highland and a lowland population of *Silene vulgaris*. *Plant Ecology*, **128**, 173–179.

710 Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham,
711 Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L.,
712 Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A.,
713 Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate
714 change. *Nature*, **427**, 145–148.

715 Thuiller, W. (2004) Patterns and uncertainties of species' range shifts under climate
716 change. *Global Change Biology*, **10**, 2020–2027.

717 Tingstad, L., Olsen, S.L., Klanderud, K., Vandvik, V. & Ohlson, M. (2015) Temperature,
718 precipitation and biotic interactions as determinants of tree seedling recruitment
719 across the tree line ecotone. *Oecologia*, **179**, 599–608.

720 Ulber, M., Gugerli, F. & Bozic, G. (2004) *EUFROGEN Technical Guidelines for Genetic*
721 *Conservation and Use for Swiss Stone Pine (Pinus cembra)*. International Plant
722 Genetic Resources Institute, Rome.

723 Uriarte, M., Anciães, M., da Silva, M.T.B., Rubim, P., Johnson, E. & Bruna, E.M. (2011)
724 Disentangling the drivers of reduced long-distance seed dispersal by birds in an
725 experimentally fragmented landscape. *Ecology*, **92**, 924–37.

726 Vitasse, Y., Hoch, G., Randin, C.F., Lenz, A., Kollas, C. & Körner, C. (2012) Tree
727 recruitment of European tree species at their current upper elevational limits in the
728 Swiss Alps. *Journal of Biogeography*, **39**, 1439–1449.

729 Vittoz, P., Rulence, B., Largey, T. & Frelechoux, F. (2008) Effects of climate and land-

730 use change on the establishment and growth of cembra pine (*Pinus cembra* L.) over
731 the altitude treeline ecotone in the Central Swiss Alps. *Arctic, Antarctic and Alpine*
732 *Research*, **40**, 225–232.

733 Vander Wall, S.B. (2002) Masting in animal-dispersed pines facilitates seed dispersal.
734 *Ecology*, **83**, 3508–3516.

735 Westcott, D. A., Bentrupperbäumer, J., Bradford, M.G. & McKeown, A. (2005)
736 Incorporating patterns of disperser behaviour into models of seed dispersal and its
737 effects on estimated dispersal curves. *Oecologia*, **146**, 57–67.

738 Zhu, K., Woodall, C.W. & Clark, J.S. (2012) Failure to migrate: lack of tree range
739 expansion in response to climate change. *Global Change Biology*, **18**, 1042–1052.

740 Zong, C., Wauters, L.A., Van Dongen, S., Mari, V., Romeo, C., Martinoli, A., Preatoni,
741 D. & Tosi, G. (2010) Annual variation in predation and dispersal of Arolla pine
742 (*Pinus cembra* L.) seeds by Eurasian red squirrels and other seed-eaters. *Forest*
743 *Ecology and Management*, **260**, 587–594.

744 Zurbriggen, N., Hättenschwiler, S., Frei, E.S., Hagedorn, F. & Bebi, P. (2013)
745 Performance of germinating tree seedlings below and above treeline in the Swiss
746 Alps. *Plant Ecology*, **214**, 385–396.

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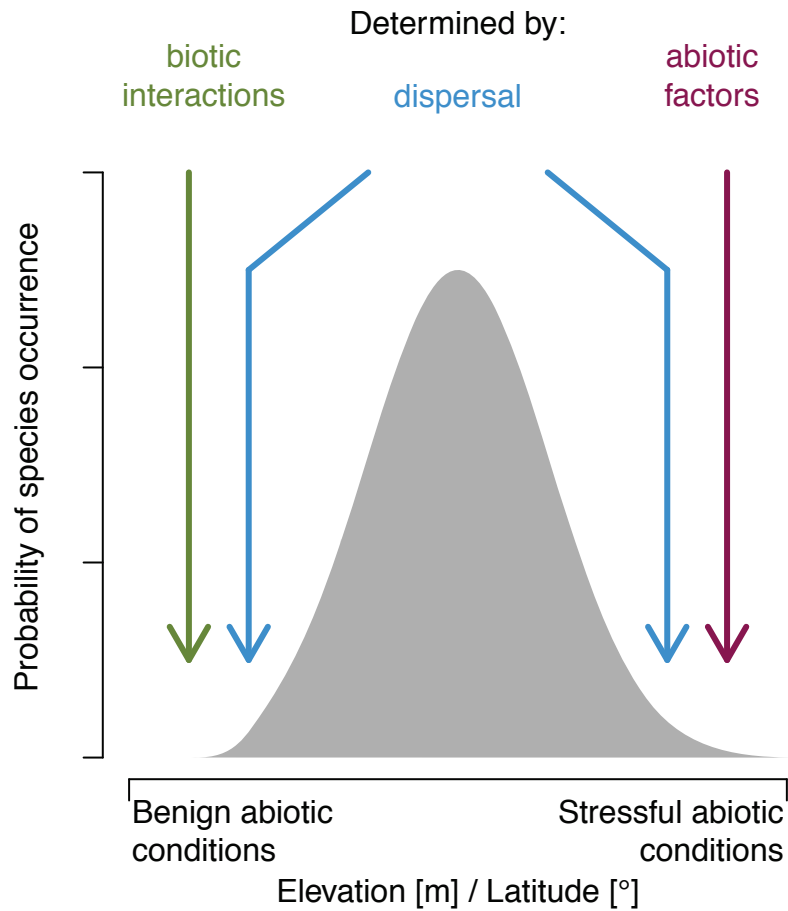
748 **Table 1.** Effects of abiotic factors, biotic interactions and seed deposition on the number
749 of juveniles a) and the probability of experimental seedling establishment b) across the
750 elevational range and at the upper and lower range of Swiss stone pine. Generalized
751 linear models were fitted assuming quasi-Poisson a) and quasi-binomial b) error
752 distributions accounting for overdispersion. Estimates present model averages from
753 qAICc-based model selection.

Model	Source of variation	Estimate	SE	p value
a) # juvenile plants	~ Seed deposition	0.85	0.27	0.002 **
Across range (1850 – 2250 m a.s.l.)	+ Understorey vegetation	1.01	0.48	0.039 *
	+ Winter temperature	0.38	0.55	0.490
	+ Summer temperature	0.03	0.21	0.883
	+ Soil moisture	0.06	0.20	0.773
	+ Region	0.04	0.20	0.848
	+ Year 2013	-0.01	0.10	0.903
	+ Year 2014	-0.00	0.09	0.984
Upper range (> 2050 m a.s.l.)	~ Seed deposition	1.95	0.55	< 0.001 ***
	+ Understorey vegetation	3.70	1.61	0.028 *
	+ Winter temperature	0.86	1.43	0.560
	+ Summer temperature	0.11	0.41	0.788
	+ Soil moisture	0.29	0.55	0.605
	+ Region	0.44	0.77	0.572
	+ Year 2013	-0.52	0.65	0.441
	+ Year 2014	0.52	0.66	0.444
Lower range (< 2050 m a.s.l.)	~ Seed deposition	0.11	0.32	0.739
	+ Understorey vegetation	-0.08	0.35	0.825

	+ Winter temperature	0.53	0.80	0.519
	+ Summer temperature	-0.68	0.89	0.452
	+ Soil moisture	0.55	1.02	0.596
	+ Region	0.51	0.67	0.458
	+ Year 2013	-0.03	0.69	0.966
	+ Year 2014	-1.55	1.35	0.259
<hr/>				
b) Seedling establishment	~ Seed predation	-2.45	0.30	< 0.001 ***
Across range	+ Understorey vegetation	0.51	0.17	0.002 **
(1850 – 2250 m a.s.l.)	+ Summer temperature	0.16	0.19	0.429
	+ Soil moisture	0.28	0.22	0.189
	+ Region	0.01	0.10	0.937
	+ Year	0.02	0.12	0.852
<hr/>				
Upper range	~ Seed predation	-1.73	0.37	< 0.001 ***
(> 2050 m a.s.l.)	+ Understorey vegetation	0.29	0.27	0.296
	+ Summer temperature	-0.00	0.13	0.987
	+ Soil moisture	0.23	0.27	0.379
	+ Region	0.05	0.15	0.752
	+ Year	0.12	0.23	0.590
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Lower range	~ Seed predation	-2.89	0.49	< 0.001 ***
(< 2050 m a.s.l.)	+ Understorey vegetation	0.11	0.22	0.598
	+ Summer temperature	0.18	0.26	0.478
	+ Soil moisture	0.06	0.18	0.730
	+ Region	-0.05	0.17	0.794
	+ Year	-0.05	0.19	0.784

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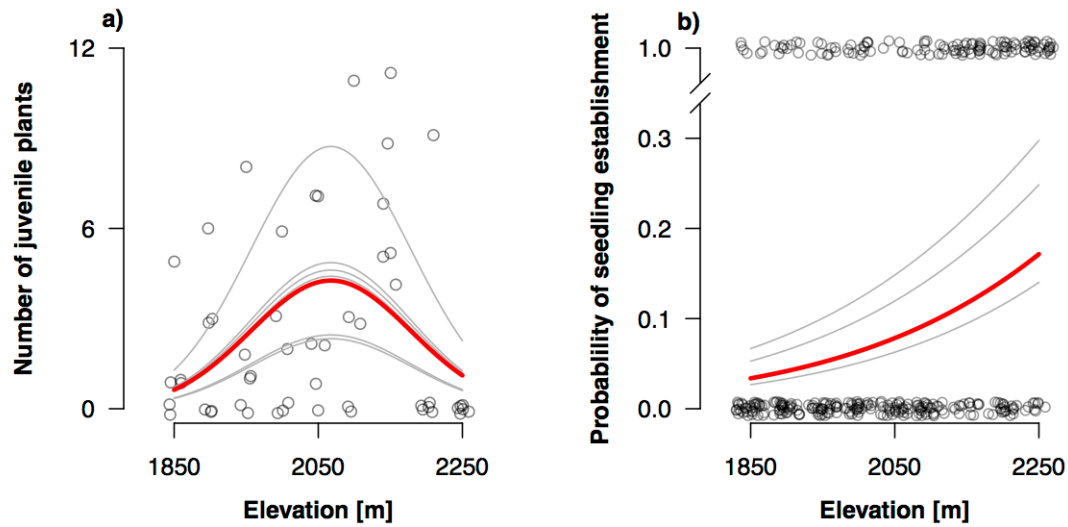
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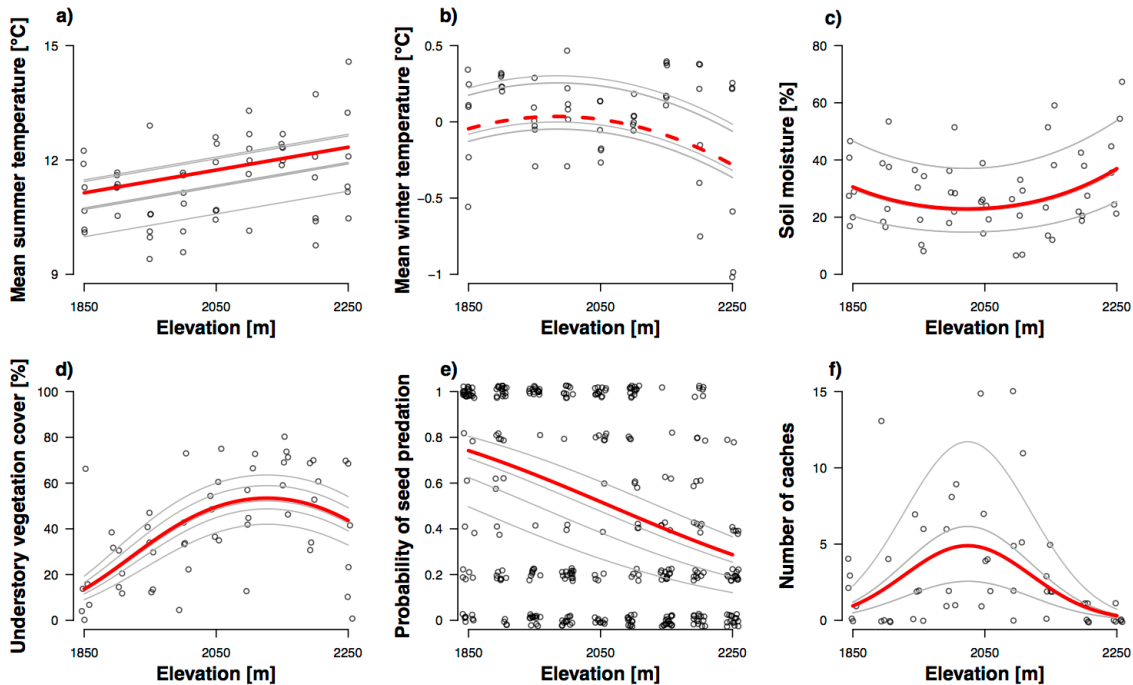
757 **Fig. 1.** Conceptual illustration of the three key determinants of species range limits:
 758 abiotic factors, biotic interactions and dispersal ability (e.g., Soberón 2007; Holt 2009).
 759 While abiotic factors are predicted to limit species distributions in particular under
 760 stressful abiotic conditions and biotic interactions should limit distributions under benign
 761 abiotic conditions (Louthan *et al.* 2015), dispersal should be limiting at both ends of
 762 species' ranges (Gaston 2009).

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765 **Fig. 2.** Natural recruitment of Swiss stone pine (a) and probability of seedling
 766 establishment in transplant experiments (b) as a function of elevation. In the generalized
 767 linear model of natural pine recruitment, a linear and a quadratic term were fitted
 768 assuming a quasi-Poisson error distribution accounting for overdispersion. In the
 769 generalized linear model of experimental seedling establishment, a linear term was fitted
 770 assuming a binomial error distribution. Circles indicate jittered raw data. Grey lines show
 771 model fit for the different valleys and years, the red line shows the overall model fit ($p <$
 772 0.05). Note break in y-axis of the experimental establishment model.

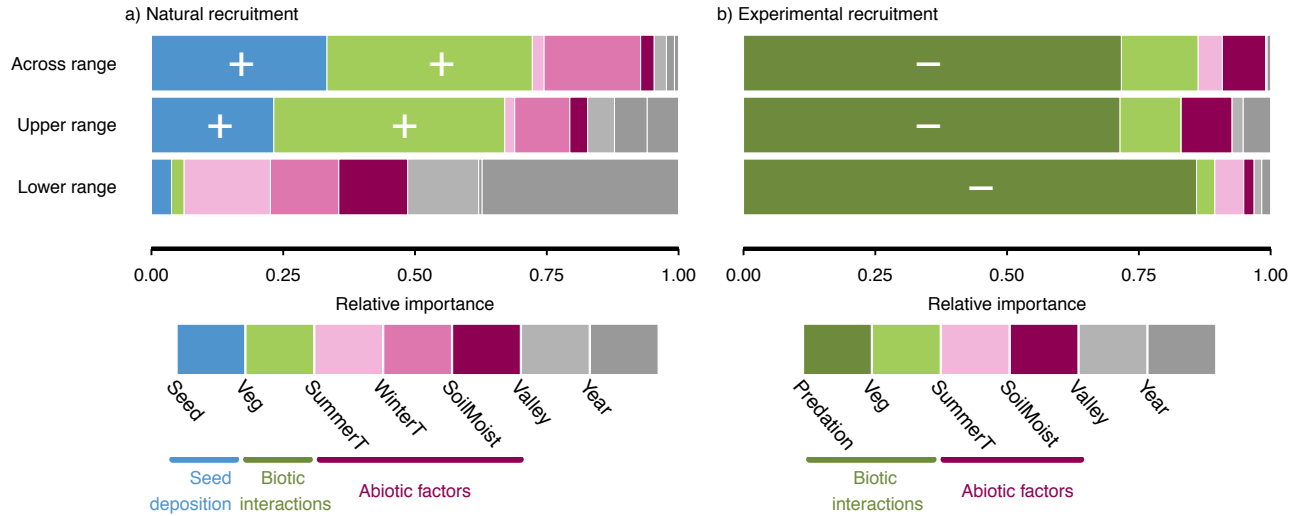


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Fig. 3. Abiotic factors (a-c), biotic interactions (d-e), and seed deposition (f) recorded in the sampling of natural pine recruitment (a-d, f) and seed transplant experiments (e) as functions of elevation; (a) mean soil surface temperature of the three warmest months, (b) mean soil surface temperature of the three coldest months, (c) proportion of soil moisture, (d) proportion of understory vegetation cover, (e) seed predation by rodents, (f) seed deposition by spotted nutcrackers. Generalized linear models were fitted using a linear (a) and a linear and quadratic term of elevation (b) and assuming a Gaussian error distribution. In (e) a linear and in (c-d) a linear and a quadratic term were fitted assuming a quasi-binomial error distribution accounting for overdispersion. In (f) a linear and quadratic term was fitted assuming a quasi-Poisson error distribution accounting for overdispersion. Circles indicate jittered raw data. Grey lines show model fit for the different valleys and years, the red line shows the overall model fit (solid: $p < 0.05$, dashed: $p > 0.05$). Further abiotic factors and biotic interactions recorded in seed

787 transplant experiments are presented in Fig. S2. Model statistics are presented in Table
788 S1 and S2.
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792 **Fig. 4.** Relative importance of abiotic factors (violet), biotic interactions (green) and seed
793 deposition (blue) on the natural recruitment of Swiss stone pine (a) and the probability of
794 seedling establishment in transplant experiments (b) across the elevational range. Models
795 included the entire elevational range (1850 – 2250 m a.s.l.) and the lower (< 2050 m
796 a.s.l.) and upper range (> 2050 m a.s.l.) of pine distribution. +/- indicate the direction of
797 the most important effects. Seed = seed deposition by spotted nutcrackers, Veg =
798 understorey vegetation cover, Predation = seed predation by rodents, SummerT = mean
799 temperature of the warmest three months, WinterT = mean temperature of the coldest
800 three months, SoilMoist = soil moisture, Year = study year, Valley = study valley.