

1       Adapted dandelions increase seed dispersal potential when they are  
2   attacked by root herbivores

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22       collected data. MP developed the time-of-flight tube. ZB, EHP, CER, CAMR, MP and ME  
23       analysed data. ZB and ME wrote the first draft of the manuscript. All authors contributed to  
24       the final version of the manuscript.

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26       Digital Repository, and the data DOI will be included in the manuscript.

27 **Abstract**

28           Plants allow their offspring to escape unfavourable local conditions through seed  
29 dispersal. Whether plants use this strategy to escape herbivores is not well understood. Here,  
30 we explore how different *Taraxacum officinale* populations modify seed dispersal in response  
31 to root herbivore attack by *Melolontha melolontha* in the field. Root herbivore attack increases  
32 seed dispersal potential through a reduction in seed weight in populations that have evolved  
33 under high root herbivore pressure, but not in populations that have evolved under low  
34 pressure. This increase in dispersal potential is associated with reduced germination,  
35 suggesting that adapted plants trade dispersal for establishment. Analysis of vegetative growth  
36 parameters suggests that increased dispersal is not the result of stress flowering. These results  
37 suggest that root herbivory selects for genotypes that increase their dispersal ability in response  
38 to herbivore attack.

## 39 **Introduction**

40           As sessile organisms, plants are bound to grow and develop where they germinate.  
41 Local conditions are therefore important determinants of plant survival and reproductive  
42 success (Kawecki & Ebert 2004, Walter et al. 2018). Although the ability of plants to move is  
43 limited, they can influence the displacement capacity of their offspring by modifying dispersal  
44 traits (Nathan & Muller-Landau 2000, Martorell & Martínez-López 2014, Teller et al. 2014).  
45 Theory suggests that whenever local conditions are unfavorable, increased seed dispersal is  
46 advantageous, as it allows the next generation to escape from the unsuitable environment and  
47 increases their chance to colonize new habitats with better conditions (Levin et al. 2003, Ronce  
48 2007). Major dispersal strategies of plants include dispersal by wind (anemochory), water  
49 (hydrochory) and animals (zoochory) (Poschlod et al. 2013).

50           Herbivores can have strong impacts on plant development and fitness and thus act as  
51 a force of natural selection (Rutter & Rausher 2004, Lau et al. 2008, Agrawal et al. 2012, Züst  
52 et al. 2012). To date, the impact of herbivores on plant dispersal remains poorly understood  
53 (de la Peña et al. 2011). Compared to aboveground herbivores, belowground herbivores are  
54 generally more limited in their mobility due to the dense nature of soil and are therefore often  
55 distributed in a patchy way (Van der Putten et al. 2001). Hence, seed dispersal may allow plants  
56 to escape belowground enemies, which may lead to selection for high dispersal genotypes by  
57 root herbivores (Van der Putten 2003). Experimental evidence for this hypothesis is currently  
58 lacking. Understanding how herbivores influence seed dispersal and establishment traits would  
59 help to elucidate their impact on plant population dynamics. In general, herbivores may affect  
60 plant dispersal strategies either by selecting for genetically fixed high dispersal genotypes or  
61 by favoring genotypes that are phenotypically plastic and increase dispersal in response to  
62 herbivore attack. Especially in stochastic environments with fluctuating herbivore pressure,  
63 inducible increase of seed dispersal distance as plastic response to herbivory may be  
64 advantageous (Jakobsson & Eriksson 2003).

65           Trade-offs between dispersal capacity and seed viability are frequent in nature. For  
66 distribution processes of wind-dispersed plant species, seed mass is often reported as a critical  
67 trait that influences both dispersal and seedling establishment. Lower seed mass typically  
68 increases dispersal (Meyer & Carlson 2001; Greene & Quesada 2005; Skarpaas et al. 2011),

69 but reduces germination and early growth (Leishman & Westoby 1994; Turnbull et al. 2004).  
70 Thus, by varying seed mass, wind-dispersed plant species may trade dispersal distance for  
71 establishment or *vice versa*. Studying seed dispersal capacity together with establishment traits  
72 is, therefore, essential to understand how seed-dispersal influences plant population dynamics.

73 Here, we studied the ecological and evolutionary impact of root herbivory on seed  
74 dispersal and fitness in the common dandelion, *Taraxacum officinale* agg. (Asteraceae). *T.*  
75 *officinale* is a species complex native to Eurasia that consists of sexual, obligate outcrossing  
76 diploids and asexual, apomictic triploids. *T. officinale* produces seeds with characteristic  
77 parachutes (pappus), which enhance uplift by the formation of separated vortex rings after  
78 detachment (Cummins et al. 2018). The seeds can be dispersed efficiently by wind and allow  
79 the plant to rapidly colonize new habitats (Tackenberg et al. 2003). A recent study found that  
80 *T. officinale* exposed to aboveground herbivory produced seeds with longer pappus and thus  
81 increased dispersal ability (de la Peña & Bonte, 2014). However, as locust exposure also  
82 results in higher biomass production, it is unclear if the change in seed morphology is a direct  
83 plastic response to herbivore exposure or an indirect consequence of changes in plant growth  
84 (de la Peña & Bonte, 2014). Furthermore, whether herbivory-induced changes in seed traits  
85 are related to the plant's evolutionary history, i.e. whether they are the result of natural selection  
86 by herbivore attack, is unclear. The larvae of *Melolontha melolontha* (Coleoptera:  
87 Scarabaeidae), also called white grubs, are the major native belowground herbivores of *T.*  
88 *officinale*. Although the larvae are polyphagous, they prefer to feed on *T. officinale* (Haus 1975,  
89 Haus & Schütte 1976). In a recent study, we showed that *T. officinale* populations that evolved  
90 under high *M. melolontha* pressure over the last decades produce higher concentrations of  
91 deterrent root secondary metabolites, suggesting that *M. melolontha* exerts positive selection  
92 pressure on *T. officinale* defenses (Huber et al. 2016b). Here, we tested the ecological and  
93 evolutionary impact of *M. melolontha* root herbivory on seed dispersal and fitness in *T.*  
94 *officinale*. We planted offspring of sympatric and allopatric *T. officinale* populations into the field  
95 and selectively infested them with *M. melolontha* larvae. We then assessed the morphological  
96 seed characteristics that determine *T. officinale* seed dispersal capacity by linking vertical seed  
97 fall rate with seed morphology. We compared dispersal and fitness related traits of seeds  
98 collected from plants under grub attack with traits of seeds collected from non-attacked plants.

99 By comparing grub-attack induced changes in seed dispersal and fitness of *T. officinale*  
100 populations with different evolutionary histories, we present evidence that *M. melolontha* affects  
101 plant fitness and dispersal through induced phenotypic plasticity that is shaped by natural  
102 selection.

## 103 **Material and Methods**

### 104 *Morphological seed characteristics underlying *T. officinale* seed dispersal capacity*

105 Average horizontal dispersal distance ( $x$ ) of wind-dispersed seeds can be calculated  
106 using a common ballistic model by multiplying the shedding height of the seed ( $H$ ) with the  
107 horizontal wind speed ( $u$ ), divided by the vertical fall rate of the seed ( $F$ ):  $x = Hu/F$  (Pasquill &  
108 Smith 1983; Brock et al. 2005). Seed fall rate is determined by seed traits such as seed mass  
109 and seed shape (Matlak 1987; Meyer & Carlson 2001; Skarpaas et al. 2011). To identify the  
110 morphological seed traits that contribute most strongly to seed dispersal potential of *T.*  
111 *officinale*, we measured the fall rate of individual *T. officinale* seeds along with morphological  
112 characteristics of individual seeds and used this data to construct a model that predicts  
113 dispersal potential from seed morphology. To cover a broad range of genotypes and  
114 environments, seeds of a total of 20 plants from the Botanical Garden of the University of Bern,  
115 Switzerland (46.95 °N, 7.43 °E, 520 m above sea level), a semi-natural grassland in Boltigen,  
116 Switzerland (46.38 °N, 7.23 °E, 1038 m above sea level), and the greenhouse (genotype A34,  
117 Verhoeven et al. 2010) were collected. Five seeds per plant were randomly selected for  
118 experiments.

119 To measure seed fall rate, we constructed a semi-automated time-of-flight system (Fig.  
120 1a). The system consists of a plexiglass tube (2 m height, 20 cm diameter, ABC-Kunststoff-  
121 Technik GmbH, Germany) that is coated with a fine metal wire grid on the inside to prevent  
122 static charges (Fig. 1a). A custom-built sampler on top of the tube ensures standardized, serial  
123 release of individual seeds into the time-of-flight tube. The sampler consists of a conveyor belt  
124 with 10 seed-containers, an electromotor to move the belt and a series of controllers to the  
125 sampler (components from Tinkerforge, Germany). A remote control allows the user to release  
126 a seed and simultaneously start a digital timer by pressing the start button. As soon as the seed  
127 crosses the finish line at the bottom of the tube, the user presses the stop button, which stops  
128 the timer and saves the time-of-flight in a small memory module. The source code of the control  
129 software and a list of the individual components can be found on Github (to be inserted at a  
130 later time). Using this system, 100 test seeds were measured three times, and average fall  
131 rates for each seed were calculated. As physiological parameters that may determine fall rate,  
132 seed weight, length and width, achene length, pappus stem length and pappus hair length were

133 determined. To standardize measures, a glass plate was put on top of the seed, and traits were  
134 measured two-dimensionally from the top. Linear regression models were then built using  
135 falling rate as response variable and combinations of seed traits as explanatory variables. We  
136 then compared the models using ANOVAs to select the best-performing model. Major variables  
137 contributing to fall rate (seed mass and pappus hair length, see results), were selected as  
138 measures of seed dispersal potential in subsequent experiments.

### 139 *Effect of root herbivory on seed dispersal and fitness*

140 To examine how root herbivory affects seed dispersal and fitness of allopatric and  
141 sympatric *T. officinale* plants, we performed a one-year experiment in a semi-natural grassland  
142 using seeds from 18 *T. officinale* populations evolved in the presence or absence of *M.*  
143 *melolontha* over the last 20 years (Table S2). A detailed description of the evolutionary history  
144 of the majority of these populations can be found in Huber et al. (2016b). In brief, nine  
145 populations originated from areas in Switzerland and Germany with high documented *M.*  
146 *melolontha* densities over the last 20 years (sympatric populations) and nine populations came  
147 from areas with no or only low *M. melolontha* abundance over the last 20 years (allopatric  
148 populations). Within each type of evolutionary history, six populations consisted of sexual,  
149 outcrossing diploids, and three populations consisted of apomictic, clonal triploids. Triploid  
150 seeds were collected directly from their respective mother plants. Diploid seeds were obtained  
151 by hand-pollination within populations. For each population, we created a seed mixture by  
152 mixing 15 seeds per plant from six randomly selected plants, giving a total of 90 seeds per  
153 population. Seed mixtures were germinated in the greenhouse and after two weeks, seedlings  
154 were individually transplanted into plastic pots (5 x 5 x 5 cm) filled with soil (Selmaterra, Bigler  
155 Samen AG, Thun, Switzerland). Three months after germination, in March 2016, the plants  
156 were introduced to the field site in Boltigen (46.38 °N, 7.23 °E, 1038 m above sea level). The  
157 field site was established in a semi-natural, organically managed grassland. *T. officinale* occurs  
158 naturally at the field site. *M. melolontha* is present in low abundance in this region.

159 For the experiment, a plot of 50 m x 15 m was fenced in to prevent cattle from entering.  
160 Plants were transplanted individually into bigger pots (13 x 13 x 13 cm) filled with soil  
161 (Selmaterra, Bigler Samen AG, Thun, Switzerland). To enable exchange of exudates, a hole  
162 was cut into the bottom of the pots (5 cm diameter) and a permeable root barrier (15 x 15 cm;

163 Trenn-Vlies, GeoTex Windhager, Switzerland) was put into the pots before transplanting. Then  
164 we excavated soil blocks (approximately 14 x 14 x 14 cm) in the field plot in seven parallel rows,  
165 with 40 cm space between the holes and 210 cm space between the rows and inserted the  
166 plants into the field in a fully randomized design (Fig. S1). This setup allowed us to embed the  
167 plants into their natural environment while controlling root herbivore exposure. To infest plants  
168 with *M. melolontha*, individual second instar larvae were introduced to half of the pots in a  
169 randomized fashion in the beginning of June 2016. *M. melolontha* larvae were collected from a  
170 field in Uri, Switzerland (46.45 °N, 8.42 °E, 822 m above sea level) and reared on carrots for 2  
171 weeks prior to the start of infestation.

#### 172 *Measurement of seed dispersal and fitness*

173 On the northern hemisphere, *T. officinale* has its main flowering peak in spring and a  
174 secondary flowering peak in late summer / early autumn (Stewart-Wade et al. 2002). We  
175 continuously monitored flower development during both flowering peaks (summer 2016 and  
176 spring 2017). Every 3-4 days, all fully ripened seeds were collected for analysis of dispersal-  
177 related seed traits. For collection, seeds of inflorescences were carefully transferred into a small  
178 paper bag without cutting or damaging the flower and flower stem heights were measured. If  
179 seeds of an inflorescence were missing from the flower heads, we estimated the percentage of  
180 remaining seeds. Seeds were stored in darkness at 4 °C until analysis.

181 For seed phenotyping, one seed head from summer 2016 and one seed head from  
182 spring 2017 were randomly chosen from each plant. Five to twelve seeds with no visible signs  
183 of damage were randomly selected from the different seed heads and phenotyped. Average  
184 seed weight and average pappus hair length per seed head were then determined. Seed fall  
185 rate was calculated as a function of seed mass and length of pappus hairs. Seed fall rate,  
186 vertical wind speed and shedding height of the seed then allowed for an estimation of the  
187 dispersal potential for each capsule. A fixed value of 23.88 cm, corresponding to the average  
188 stem height in summer 2017, was chosen as a release height for our calculations. We used a  
189 constant release height, as the variation in stem height between genotypes recorded in summer  
190 2017 was minimal compared to the variation in seed traits (Table S1, Fig. S2). For wind speed,  
191 we used 2 m/s, which is the yearly average wind speed in 2016 recorded by the nearest  
192 SwissMetNet surface weather station (Boltigen, 46.37 °N, 7.23 °E, 820 m above sea level).



193 To determine if the dispersal potential and the number of viable offspring per plant are  
194 correlated, we measured germination rates of collected seeds in a climate chamber in August  
195 2017 (temperature at day 22 °C and at night 18 °C; 16 h light and 6 h darkness; 65% humidity;  
196 light intensity approximately 120  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). From each phenotypic analysed seed capsule,  
197 ten seeds were randomly selected and equally distributed in a small pot (5.5 cm diameter) filled  
198 with moist seedling substrate. The pots were watered regularly and checked daily. Each day  
199 we recorded the number of germinated seeds per pot and after 14 days, germination rate was  
200 calculated by dividing the number of emerged seedlings through the number of seeds. By  
201 multiplying germination rate with the number of flowers per plant and number of seeds per head  
202 per plant, we then estimated the number of viable offspring per plant as a proxy for plant fitness  
203 (Erb 2018).

#### 204 *Measurement of vegetative growth*

205 For each of the 797 plants in the field experiment, we determined plant vegetative  
206 growth by counting the number of leaves and measuring the length of longest leaf as a proxy  
207 for plant performance (Huber et al. 2016a). Plant performance was determined on a monthly  
208 basis from June 2016 to June 2017, with the exception of January-March 2017, when snow  
209 cover prevented measurements. In mid-July 2016, the field was mown according to normal  
210 agricultural practice. Before mowing, we individually collected the aboveground biomass of  
211 each plant. Shoots were cut 5 cm above ground, put into paper bags, dried in an oven at 80 °C  
212 until constant mass was reached and weighted. In June 2017, the experiment was terminated,  
213 and aboveground biomass was measured again.

#### 214 *Statistical analyses*

215 All statistical analyses were performed in R 3.3.3 (R Core Team 2017). To predict seed  
216 fall rate, 'Seed mass' and 'Pappus hair length' were used in a linear regression model. No  
217 interactions were included in the model. The predictive power of the model was evaluated using  
218 k-fold cross validation. For the linear regression model, the function 'lm' of the stats package  
219 was used (R Core Team 2017) and the validation of the predictive power was done with the  
220 function 'train' of the 'caret' package (Kuhn 2008).

221 For the analysis of seed traits, mean values per population were calculated separately  
222 for plants with and without grub infestation. Mean population values were then examined with

223 linear models. Multiple linear models were built with ‘Herbivory’ x ‘Evolutionary history’ x ‘Ploidy  
224 level’ as explanatory variables and each recorded seed parameter as response variable  
225 (‘Flower heads’, ‘Seeds per head’, ‘Pappus hair length’, ‘Seed mass’, ‘Dispersal potential’,  
226 ‘Germination rate’ and ‘Offspring per plant’). For analysis of vegetative growth, a linear model  
227 was employed on ‘Biomass’ as response variable with ‘Herbivory’ x ‘Evolutionary history’ x  
228 ‘Ploidy level’ as explanatory variables. Further, ‘Length of longest leaf’ was analysed as  
229 response variable in two linear models with ‘Herbivory’ x ‘Evolutionary history’ x ‘Time’ as  
230 explanatory variables separately for diploid and triploid plants. All models were examined using  
231 the function ‘plotresid’ (package ‘RVAMemoire’ (Hervé 2018)). Significance of explanatory  
232 variables was tested using the function ‘Anova’ (package ‘car’ (Fox & Weisberg 2011)) and  
233 results were plotted using the package ‘ggplot2’ (Wickham 2009). Similar results were obtained  
234 with models for values of individual plants, which included ‘Population’ as random factor,  
235 compared to models for mean values per population.

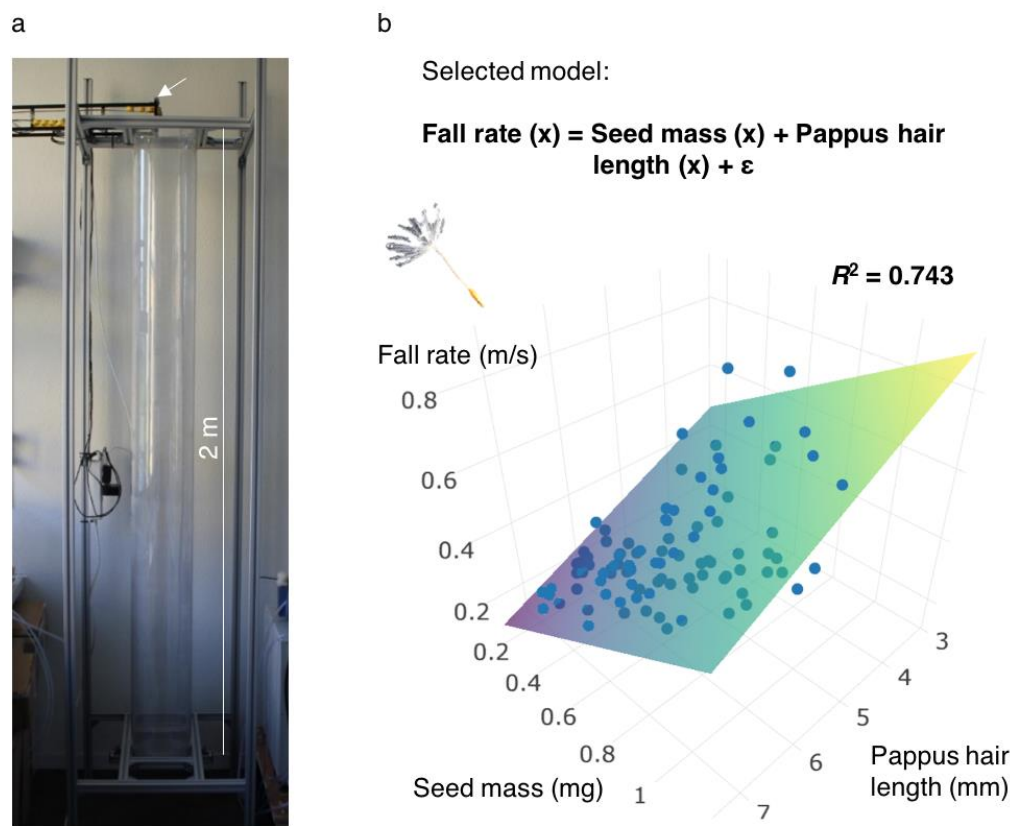
236 To investigate if changes in seed mass are linked to changes in biomass, correlation  
237 strength between ‘Seed mass’ and Biomass’ was analysed separately for seeds from summer  
238 2016 and spring 2017. Further, to examine if there is a trade-off regarding the plant’s investment  
239 into seed production optimized for dispersal or germination, correlation strength between  
240 ‘Dispersal potential’ and ‘Germination rate’ was analysed separately for seeds from summer  
241 2016 and spring 2017.

242 To investigate direct and indirect relationships between and within analysed seed and  
243 growth traits, we used structural equation modelling (SEM) (Shipley 2016). We developed an  
244 a priori model based on the results of our data analysis and on physiological and ecological  
245 knowledge, which includes all measured plant traits except the estimated variables ‘Dispersal  
246 potential’ and ‘Offspring per plant’, as those were calculated out of other seed traits. We  
247 hypothesized direct effects of season (summer 2016 vs. spring 2017) on the measured seed  
248 and flower traits and on biomass production. Further, we assumed direct effects of biomass on  
249 the measured seed and flower traits and an indirect effect of biomass on germination rate  
250 through seed mass and pappus hair length. In addition, we hypothesized an indirect effect of  
251 number of flower heads per plant and number of seeds per head on germination rate through  
252 seed mass and pappus hair length. We assumed bidirectional links between seed mass and

253 pappus hair length and between number of flower heads per plant and number of seeds per  
254 head. To avoid large differences in the variances among the variables we first scaled all  
255 variables to an equal range by dividing through powers of 10 if necessary. We then used the R  
256 package 'lavaan' (Rosseel 2012) for fitting and testing the SEM. Model fit indices (CFI = 0.999,  
257 TLI = 0.996, RMSEA = 0.018) indicated good model fit, so maximum likelihood was used to  
258 estimate standardized path coefficients.

## 259 Results

### 260 Seed weight and pappus hair length determine dispersal potential of *T. officinale* seeds



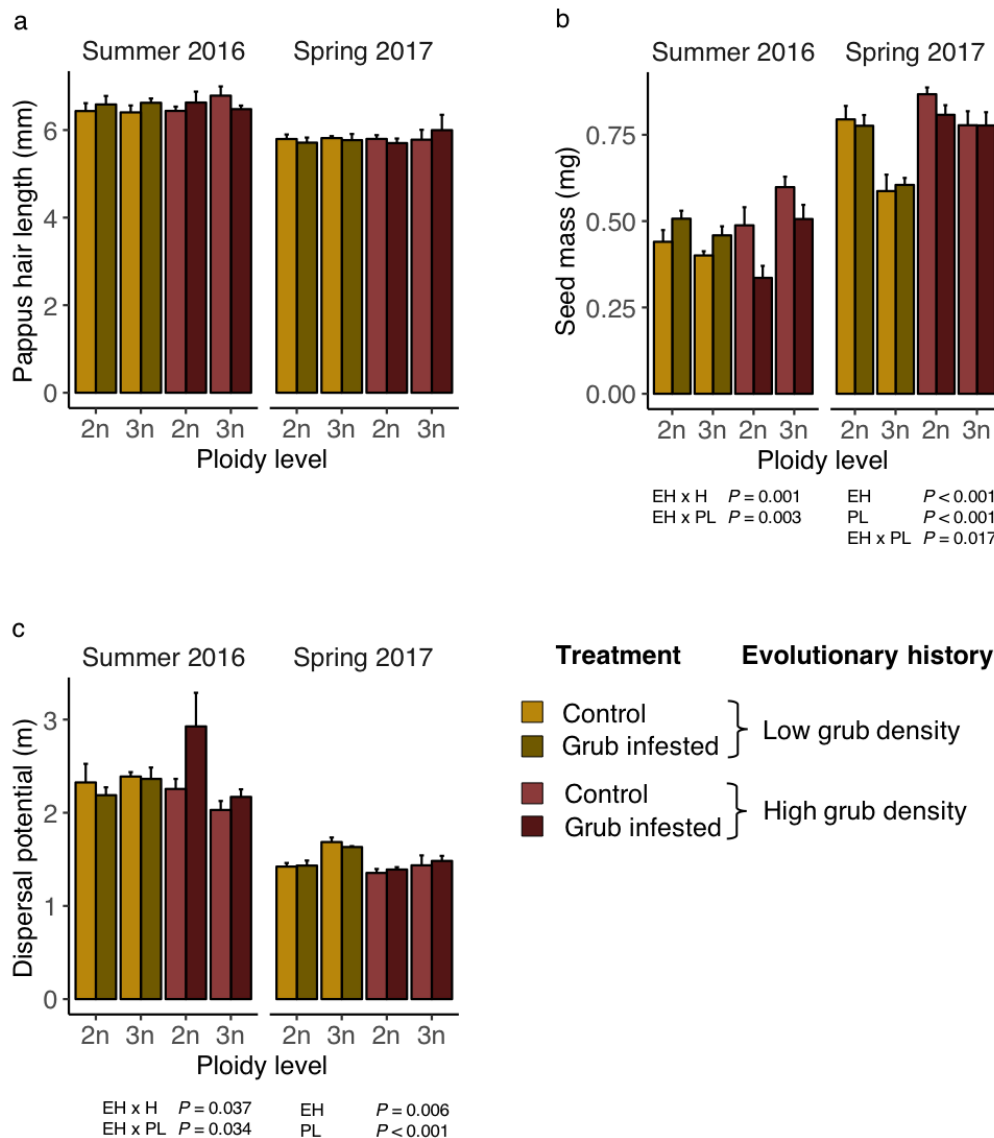
261 **Fig. 1 Seed mass and pappus hair length determine dispersal potential of dandelion**  
262 **seeds.** (a) Photograph of a custom-built plexiglass time-of-flight tube with semi-automatic seed  
263 dispenser (white arrow) to determine fall rates of individual dandelion seeds. (b) A linear model  
264 predicts seed fall rate using seed mass and pappus hair length. The adjusted  $R^2$  of the model-  
265 fit is displayed.

266 Comparisons of multiple linear regression models revealed that vertical seed fall rate  
267 of *T. officinale* – and subsequently seed dispersal potential - is predicted well by seed mass  
268 combined with pappus hair length. The final model ( $\text{Fall rate (x)} = \text{Seed mass (x)} + \text{Pappus hair}$   
269  $\text{length (x)} + \epsilon$ ) showed high predictive power using these two parameters ( $R^2 = 0.743$ , Fig. 1b).  
270 While seed mass increases fall rate and thus decreases dispersal potential, the length of the  
271 pappus hair decreases fall rate and thus increases dispersal potential.

### 272 Root herbivory attack increases seed dispersal potential in sympatric populations

273 During the summer flowering period, *M. melolontha* infestation did not affect pappus  
274 hair length (Fig. 2a), but reduced the mass of *T. officinale* seeds (Fig. 2b), resulting in increased  
275 dispersal potential compared to control plants (Fig. 2c). This response was observed in

276 sympatric, but not allopatric populations (LM, factor 'EH x H',  $P = 0.001$ , Fig. 2b; respectively  
 277 LM, factor 'EH x H',  $P = 0.037$ , Fig. 2c). During the spring flowering period, no effect of root  
 278 herbivory on seed traits was detected (Table S1).  
 279



280

281 **Fig. 2 Root herbivore attack increases seed dispersal potential in sympatric dandelion**  
 282 **populations.** Compared to allopatric populations (yellow bars), sympatric populations (red  
 283 bars) developed lighter seeds with increased dispersal potential under root herbivory. Seed  
 284 mass (a), pappus hair length (b) and dispersal potential (c) of seeds collected from plants with  
 285 (hatched bars) and without (plain bars) root herbivory by *M. melolontha* are shown. Mean  
 286 values of population means ( $N = 3-6$  populations) and standard errors ( $\pm$  SE) are indicated.  $P$ -  
 287 values from linear models are shown (significant effects only). EH: Evolutionary history of  
 288 population. H: Root herbivory treatment. PL: Ploidy level. 2n: Diploid populations. 3n:  
 289 triploid populations.  
 290

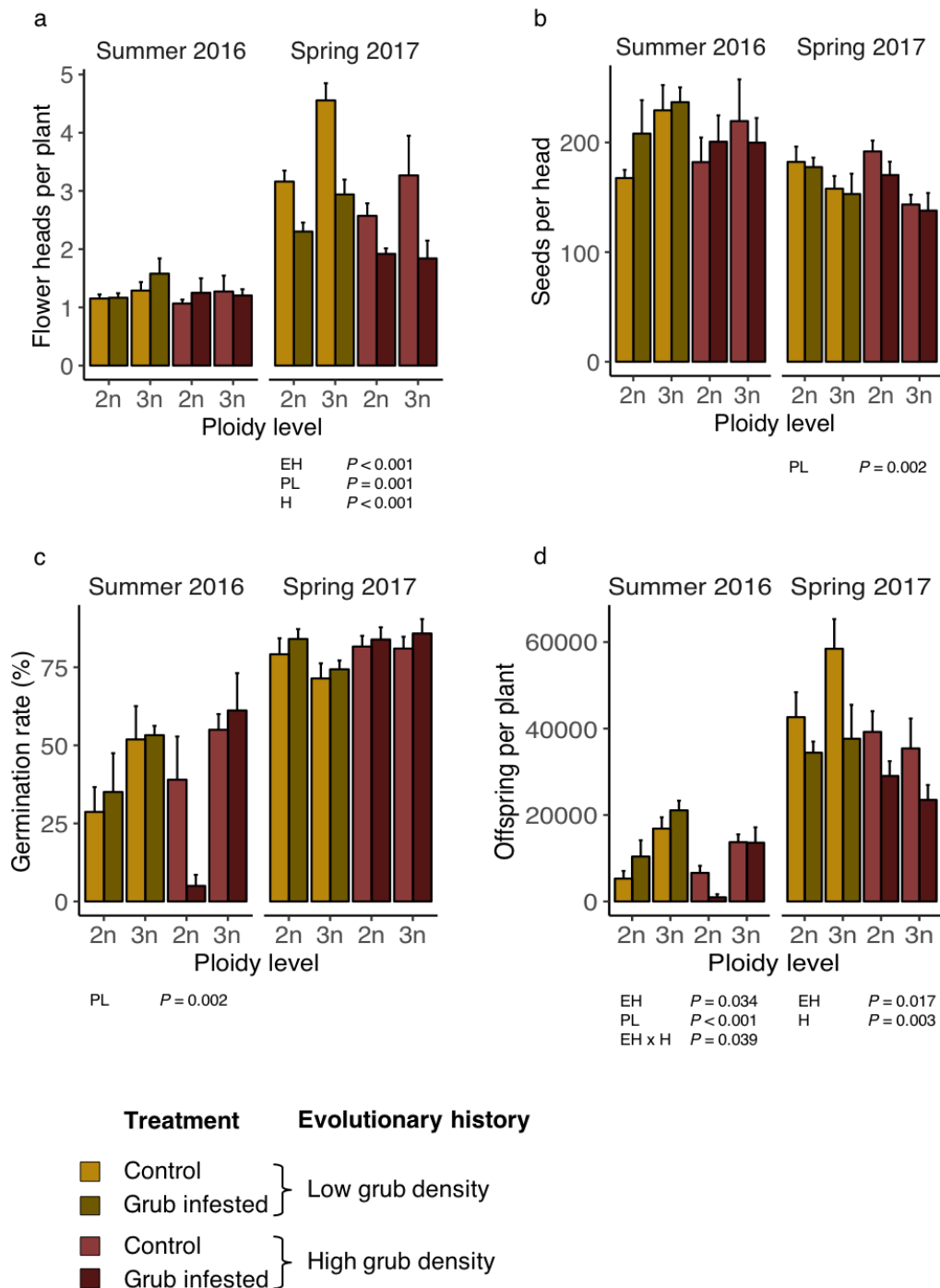
291 *Evolutionary history and cytotype interact to determine seed dispersal potential*

292 We detected significant effects of evolutionary history and cytotype on seed mass and  
293 dispersal potential (Fig. 2). During the summer flowering period, seeds of sympatric triploids  
294 were heavier and had a lower dispersal potential than seeds of sympatric diploids, while the  
295 opposite was the case for allopatric populations (LM, factor 'EH x PL',  $P = 0.003$ , Fig. 2b;  
296 respectively LM, factor 'EH x PL',  $P = 0.034$ , Fig. 2c). During the spring flowering period, seeds  
297 of sympatric populations were heavier and had a lower dispersal potential than seeds of  
298 allopatric populations (LM, factor 'EH',  $P < 0.001$ , Fig. 2b; respectively LM, factor 'EH',  $P =$   
299  $0.006$ , Fig. 2c), and triploid seeds were generally lighter and thus had a higher dispersal  
300 potential than diploid seeds (LM, factor 'PL',  $P < 0.001$ , Fig. 2b; respectively LM, factor 'PL',  $P$   
301  $< 0.001$ , Fig. 2c).

302 *Root herbivory reduces plant fitness*

303 During the summer flowering period, root herbivory did not significantly affect the  
304 number of flower heads, the number of seeds or the percentage of germinating seeds per plant  
305 (Fig. 3a-c). The total number of offspring per plant, which was calculated by multiplying flower  
306 heads, seeds per head and germination rate, however, was reduced by *M. melolontha* attack  
307 in sympatric, but not in allopatric populations (LM, factor 'EH x H',  $P = 0.039$ , Fig. 3d). In spring,  
308 *M. melolontha* reduced the number of flower heads and total viable offspring per plant  
309 independently of the other factors (LM, factor 'H',  $P < 0.001$ , Fig. 3a; respectively LM, factor  
310 'H',  $P = 0.003$ , Fig. 3d). Evolutionary history and cytotype also affected plant fitness traits (Fig.  
311 3). Triploid seeds from the summer flowering period germinated better, leading to a higher  
312 number of offspring per plant (LM, factor 'PL',  $P = 0.002$ , Fig. 3c; respectively LM, factor 'PL',  $P$   
313  $< 0.001$ , Fig. 3d). During the spring flowering period, triploids produced more flower heads per  
314 plant (LM, factor 'PL',  $P = 0.001$ , Fig. 3a), but fewer seeds per flower head (LM, factor 'PL',  $P$   
315  $= 0.002$ , Fig. 3b), and showed no difference in germination rate and offspring per plant (Fig. 3c-  
316 d). Sympatric populations produced fewer flowers than allopatric populations during the spring  
317 flowering period, and the number of viable offspring was lower for sympatric populations than  
318 allopatric populations (LM, factor 'EH',  $P < 0.001$ , Fig. 3a; respectively LM, factor 'EH',  $P =$   
319  $0.017$ , Fig. 3d).

320



321 **Fig. 3 Root herbivore attack reduces plant fitness.** Flower heads per plant (a), seeds per  
 322 head (b), germination rate (c) and offspring per plant (d) of plants with (hatched bars) and  
 323 without (plain bars) root herbivory by *M. melolontha* are shown. Mean values of population  
 324 means ( $N = 3-6$  populations) and standard errors ( $\pm$  SE) are indicated.  $P$ -values from linear  
 325 models are displayed (significant effects only). EH: Evolutionary history of population. H: Root  
 326 herbivory treatment. PL: Ploidy level. 2n: Diploid populations. 3n: Triploid populations.

327 *Root herbivory decreases vegetative growth*

328 To determine whether reduced plant performance upon *M. melolontha* attack may  
329 explain the changes in seed mass and subsequently in dispersal potential in sympatric  
330 populations, we measured the impact of *M. melolontha* attack on shoot growth and biomass  
331 and then correlated shoot biomass with seed mass. The length of the longest leaf, a proxy for  
332 biomass accumulation (Huber et al. 2016a) varied through the season and was significantly  
333 reduced by *M. melolontha* infestation (Fig. 4a). Shoot biomass was significantly reduced in  
334 plants attacked by *M. melolontha* during both sampling periods (LM, factor 'Herbivory',  $P =$   
335 0.009 and LM, factor 'Herbivory',  $P = 0.047$ , Fig. 4b). Further, during the summer sampling  
336 period, triploids produced more biomass than diploids (LM, factor 'Ploidy level',  $P < 0.001$ , Fig.  
337 4b). However, none of these effects was different between sympatric and allopatric populations,  
338 suggesting that the increase in seed dispersal capacity upon *M. melolontha* attack in sympatric  
339 populations is not due to a general plant stress response.

340 *Correlations between vegetative growth, fitness and dispersal*

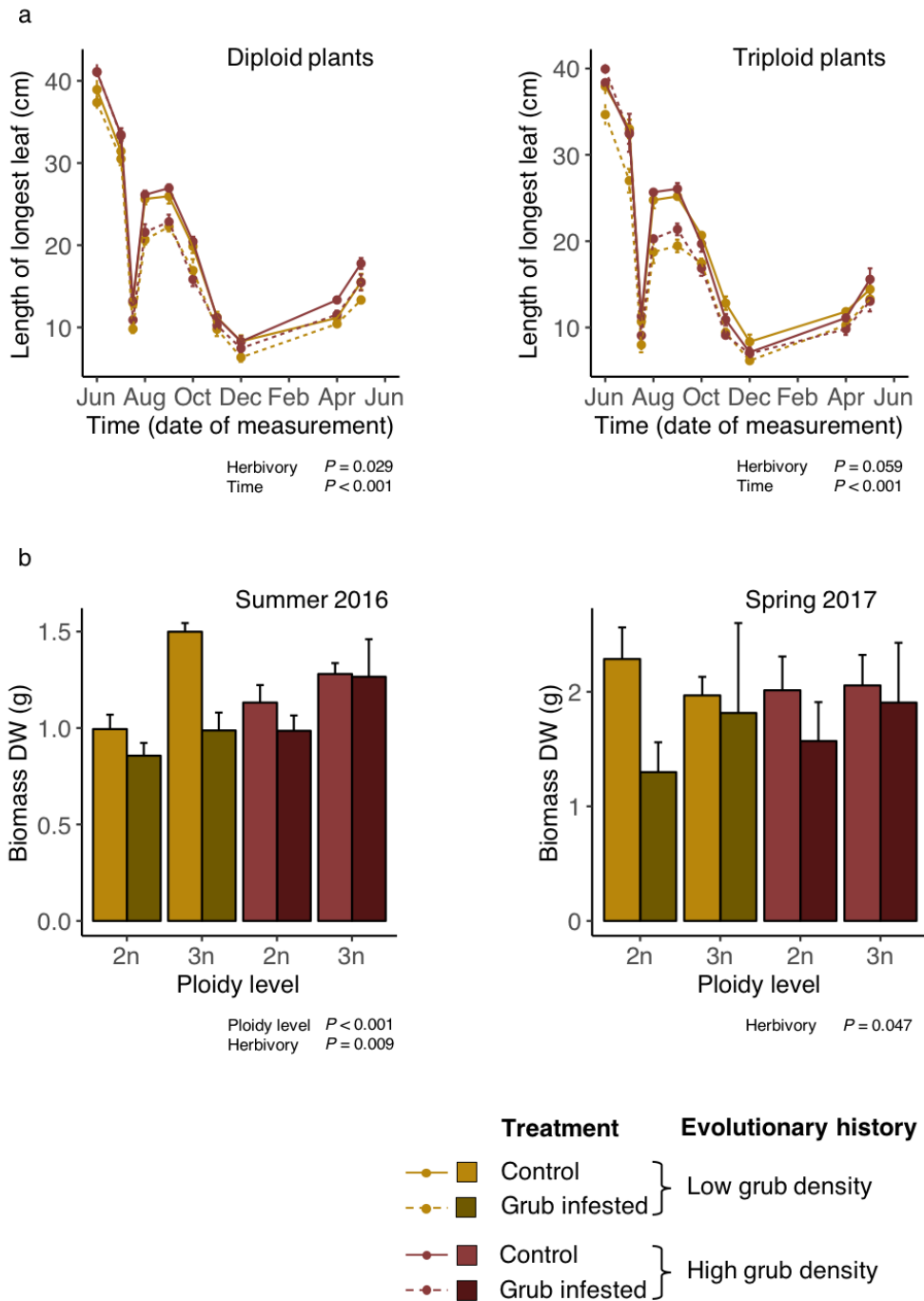
341 Structural equation modelling (SEM) revealed that the sampling period ('Season') had  
342 an influence on both vegetative and generative traits. In summer 2016, *T. officinale* plants  
343 produced more seeds per head and seeds with longer pappus hair. In spring 2017, plants  
344 produced more biomass, more flower heads per plant, heavier seeds with higher germination  
345 rate, but shorter pappus hair (Fig. 5a).

346 Across all plants, vegetative biomass production explained seed mass and pappus hair  
347 length (Fig. 5a). However, across populations and analysed for each sampling season  
348 separately, shoot biomass was not correlated with average seed mass and hence dispersal  
349 potential ( $R^2 = 0.009$ ,  $P = 0.593$  and  $R^2 = 0.080$ ,  $P = 0.095$ , Fig. S3). Seed mass explained  
350 pappus hair length and germination rate. (Fig. 5a). Pappus hair length was a negative predictor  
351 of germination rate. The number of flowers per head was a negative predictor of seed mass,  
352 while the number of seeds per head was a positive predictor of seed mass and pappus hair  
353 length (Fig. 5a).

354 To further understand the relationship between dispersal potential (calculated from  
355 seed mass and pappus hair length) and total offspring per plant (calculated from flower heads,  
356 seeds per head and germination rate), we correlated these two parameters. Dispersal potential

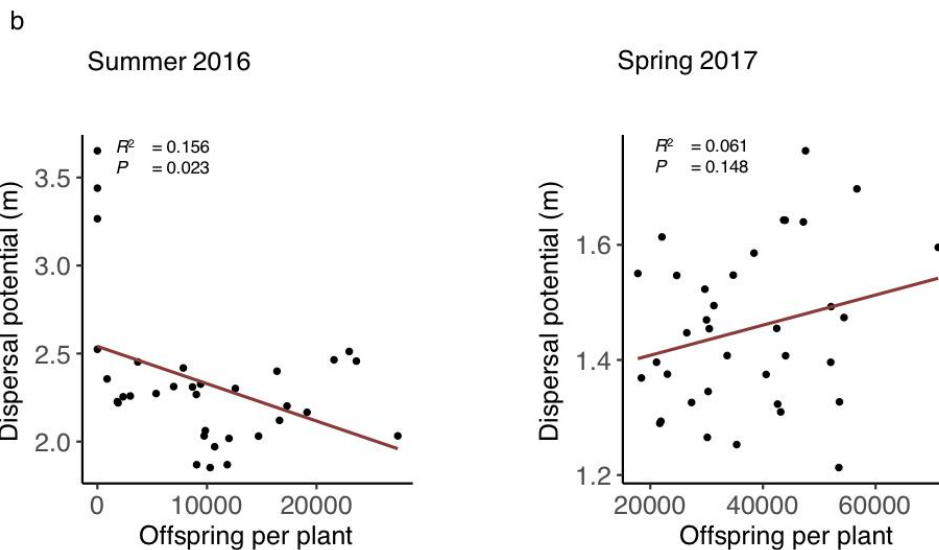
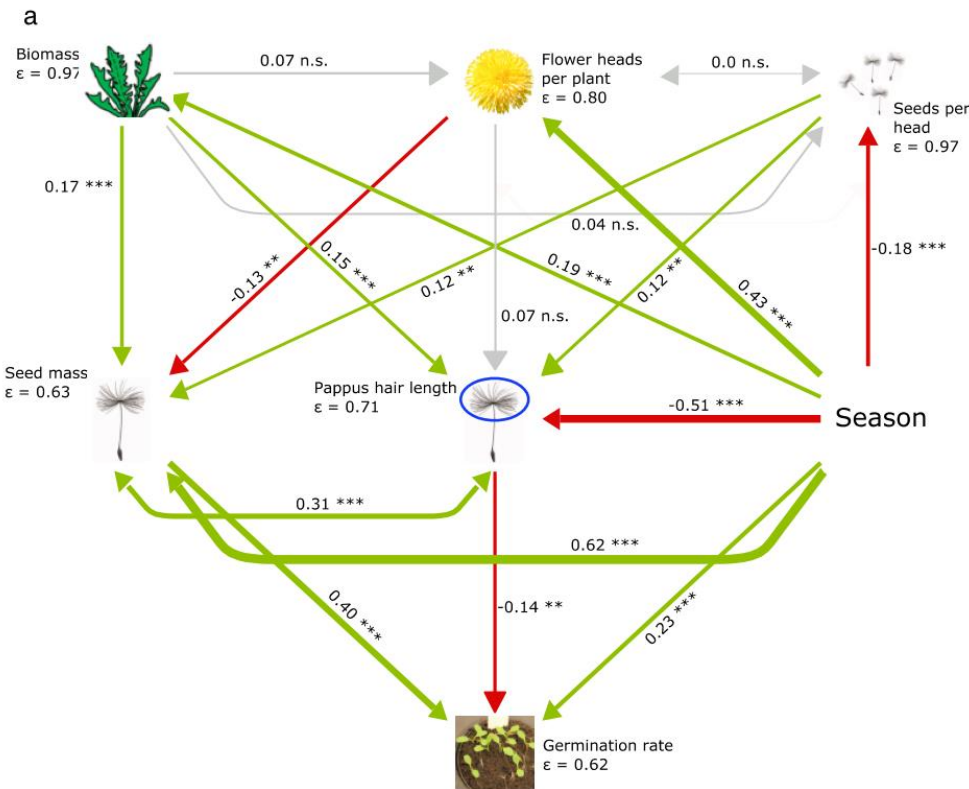


357 and offspring per plant were negatively correlated for the summer flowering period, but not the  
358 spring flowering period ( $R^2 = 0.156$ ,  $P = 0.023$  and  $R^2 = 0.061$ ,  $P = 0.148$ , Fig. 5b). Together,  
359 these results show that *T. officinale* dispersal and reproductive potential differ markedly  
360 between the summer and spring flowering periods, and that there seems to be a tradeoff  
361 between dispersal and reproduction during the summer flowering period, which is mostly driven  
362 by seed mass, which increases germination, but decreases dispersal potential.



363

364 **Fig. 4 Rood herbivore attack reduces vegetative growth.** (a) Length of longest leaf in diploid  
 365 and in triploid populations under infestation with *M. melolontha* (dashed lines) compared to  
 366 plants without root herbivory (full lines). Vegetation was cut back at the end of July. (b) Above  
 367 ground biomass decreased under root herbivory (hatched bars) compared to biomass of plants  
 368 without root herbivory (plain bars). Mean values of population means ( $N = 3-6$  populations) and  
 369 standard errors ( $\pm$  SE) are shown.  $P$ -values from linear models are displayed (significant effects  
 370 only). 2n: Diploid populations. 3n: Triploid populations.  
 371



372  
 373 **Fig. 5 Dispersal and establishment are negatively correlated during the summer**  
 374 **flowering period** (a) Structural equation model showing pathways between phenotypic plant  
 375 parameters. Positive links are indicated by green arrows and negative links are indicated by  
 376 red arrows. Grey arrows represent non-significant links. Red arrows coming from 'Season'  
 377 represent stronger effects of sampling period 'summer 2016', whereas green arrows coming  
 378 from 'Season' represent stronger effects of sampling period 'spring 2017'. Line thicknesses of  
 379 arrows correspond to the effect size given by their standardized path coefficients, which are  
 380 shown next to each path. Asterisks next to path coefficients indicate  $P$ -values (\*\* $P < 0.01$ ;  
 381 \*\* $P < 0.01$ ; \* $P < 0.05$ ; n.s.  $P \geq 0.05$ ). Residual variance ( $\epsilon$ ) is given for all response variables.  
 382 (b) Strength of correlation between dispersal potential and offspring per plant for seeds  
 383 collected in summer 2016 and in spring 2017. Linear regression lines of population means and  
 384 corresponding  $R^2$ - and  $P$ -values are shown.  
 385

## 386 Discussion

387 Plants can escape from unfavourable environments through seed dispersal. How seed  
388 dispersal capacity is affected by herbivory, however, is not well understood. Here, we show  
389 that *T. officinale* plants from sympatric, but not allopatric populations, increase their seed  
390 dispersal potential upon root herbivore attack in the field by reducing seed mass at the expense  
391 of the number of viable offspring. Below, we discuss the mechanisms and ecological  
392 implications of these findings.

393 Whether seed dispersal is an effective strategy to escape from hostile environments  
394 depends on the distance that can be covered by the dispersing seeds relative to the size of the  
395 unfavorable habitat. Attack by root-feeding *M. melolontha* larvae resulted in increased seed  
396 dispersal potential in sympatric *T. officinale* plants during the summer flowering period.  
397 Assuming an average wind speed of 2m/s, dispersal potential for grub-attacked sympatric  
398 populations can be estimated to exceed dispersal of non-attacked populations by 41 cm. As  
399 third instar larvae, *M. melolontha* can move up to 20 cm per day (Hasler 1986). An increased  
400 seed dispersal distance of 41 cm may therefore not be sufficient to escape a patch with high  
401 *M. melolontha* density. However, chances for long-distance dispersal induced by vertical wind  
402 turbulence are also higher for seeds with lower falling velocity. Although long-distance dispersal  
403 is relatively rare, producing seeds with lower fall rates does enhance the probability of *T.*  
404 *officinale* offspring to be dispersed over hundreds of meters under favorable conditions, which  
405 may allow the plant's offspring to escape from heavily root herbivore infested patches.

406 Theory predicts that increased seed dispersal is advantageous under locally stressful  
407 conditions and may therefore be adaptive (Levin et al. 2003, Ronce 2007). To which extend the  
408 herbivory-induced changes in seed traits observed here represents a form of adaptive plasticity  
409 is not fully clear. Adaptive plasticity, defined as plasticity maintained through natural selection,  
410 should lead to increased fitness (Miner et al. 2005). However, dispersal distance *per se* is not  
411 a direct fitness measurement, as the benefit of dispersal depends on the environmental context  
412 (van Kleunen & Fischer 2005; Teller et al. 2014). In this context, it is worth noting that we  
413 observed an increase in seed dispersal potential during grub attack in sympatric *T. officinale*  
414 populations, which have evolved in the presence of *M. melolontha* over the last decades, but  
415 not in allopatric populations that have not been under white grub pressure. This result supports

416 the notion that seed dispersal traits are subject to natural selection (Cheptou et al. 2008; Ronce  
417 2007; García-Verdugo et al. 2017; Saastamoinen et al. 2018) and indicates that root herbivores  
418 may exert selection pressure on seed phenotypic plasticity.

419 In general, the seed dispersal capacity of a plant may increase under unfavorable  
420 environmental conditions due to “stress flowering”, leading to suboptimal seed development  
421 and, thus, lighter seeds (Germain & Gilbert 2014, Begcy & Walia 2015). Our results suggest,  
422 however, that physiological stress is unlikely to explain the increase in dispersal potential in  
423 root-herbivore attacked dandelions. We found that *M. melolontha* attack reduces growth and  
424 biomass accumulation of dandelion plants, but that these effects are similar in sympatric and  
425 allopatric populations. Thus, we expect that the extent of stress that is imposed by root  
426 herbivory does not differ between allopatric and sympatric populations. As only sympatric  
427 populations adjust their seed phenotype upon root herbivore attack, we, therefore, propose that  
428 this change represents a form of herbivore-induced plant response rather than a secondary  
429 effect of physiological stress.

430 Seed mass influences dispersal potential and germination ability in opposite directions  
431 and therefore represents a physiological trade-off. Many studies empirically support this  
432 assumption (e.g. Soons & Heil 2002; Jakobsson & Eriksson 2003). Our study confirms that  
433 vertical falling velocity and hence distribution distance of *T. officinale* seeds as well as  
434 germination rate are strongly linked to seed mass. The capacity to disperse seeds thus comes  
435 with a reduction in total viable offspring. Thus, dandelions may trade establishment ability  
436 against higher dispersal potential under root herbivore attack. The high cost of higher dispersal  
437 likely contributed to the inducibility of this phenomenon. Interestingly we found a significant  
438 negative relationship between dispersal distance and number of viable offspring for the first  
439 sampling period in summer, when root herbivory had a significant effect on dispersal, but no  
440 significant link in the second sampling period, where root herbivory did not change seed  
441 phenotypes. Thus, the negative relationship between dispersal and seed mass seems to be  
442 context dependent and more strongly expressed under environmental stress.

443 Herbivores exert selection pressure on plants, leading to the evolution of tolerance and  
444 defense strategies (Núñez-Farfán et al. 2007). Earlier work demonstrated that sympatric  
445 dandelion populations that grow in the presence of *M. melolontha* produce higher amounts of

446 repellent root sesquiterpene lactones, which may benefit them by becoming less attractive to  
447 *M. melolontha* (Huber et al. 2016b). The experimental setup in this study controlled for these  
448 potential effects by confining root herbivores to individual dandelion plants. Our results suggest  
449 that, when *M. melolontha* larvae do not have a choice between different plants, there is no  
450 direct benefit to producing the repellent chemicals. On the contrary, sympatric populations  
451 suffered from the same biomass reduction and did not produce more flowers or seeds under  
452 root herbivore attack than allopatric populations. In combination with our earlier studies (Huber  
453 et al. 2016a, Huber et al. 2016b, Bont et al. 2017), these results suggest that high herbivore  
454 pressure selects for repellent root chemicals and higher dispersal potential, but not stronger  
455 resistance or tolerance in dandelion. These results emphasize the need to evaluate the  
456 evolution of plant defense strategies in a community context (Agrawal et al. 2012, Poelman &  
457 Kessler 2016) and to include seed and dispersal traits into these analyses (Erb 2018).

458         Through feeding on roots, belowground insects can severely impair plant performance.  
459 From an evolutionary point of view, presence of root-feeders may therefore act as selective  
460 force on plant traits involved in seed distribution and establishment. In our study, exposure to  
461 *M. melolontha* resulted in reduced flower production, but it also resulted in the production of  
462 better dispersible seeds - depending on the sampling period and the evolutionary history of *T.*  
463 *officinale*. Thus, our findings suggest an important, but context-dependent influence of root  
464 herbivory on plant reproduction and dispersal traits.

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596 **Supporting information**

597 Additional supporting information may be downloaded via the online version of this  
598 manuscript.