

1 **Optimal foraging by herbivores maintains polymorphism in defence in a**  
2 **natural plant population**

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## 25 SUMMARY

26 1. Many species of plants and animals exhibit polymorphism for defensive traits. Adaptive  
27 foraging by natural enemies has long been hypothesized to maintain such polymorphism, but  
28 this has not been clearly demonstrated in a natural prey or host population.

29 2. The purpose of this study was to address whether the brassica leaf beetle *Phaedon*  
30 *brassicae* promotes the maintenance of defence polymorphism in the trichome-producing  
31 (hairy) and trichomeless (glabrous) morphs of *Arabidopsis halleri* subsp. *gemmifera*. Here,  
32 we modelled foraging behaviours of herbivores and demography of the host plant. Then, we  
33 estimated the model parameters based on the likelihood of observed data from a natural *A.*  
34 *halleri* population.

35 3. The patterns of leaf damage to hairy and glabrous plants were well explained when we  
36 presumed the optimal diet choice by *P. brassicae*. The observed dynamics in the plant  
37 number and morph frequency were well supported by the model with the estimated parameter  
38 values. Our numerical analysis showed that the optimal diet choice by *P. brassicae* caused a  
39 negative frequency-dependent selection on trichrome dimorphism. The coexistence of two  
40 morphs was allowed over a wide range of herbivory pressure and the cost of defence.

41 4. These results indicate that the optimal diet choice by *P. brassicae* contributes to the  
42 coexistence of hairy and glabrous *A. halleri*. While species interaction and stochastic  
43 dispersal are both involved in polymorphism dynamics in the field, our findings suggest that  
44 the role of consumer behaviours in the maintenance of defence polymorphism may be more  
45 important than currently appreciated.

46

47 **Keywords:** *Arabidopsis halleri* subsp. *gemmifera*; Associational effects; Genetic variation;  
48 Herbivory; Optimal diet choice; Plant defence

## 49 INTRODUCTION

50 Many plant and animal species develop defence traits against their natural enemies. Genetic  
51 variation within species in defence traits has often been reported for both chemical and  
52 morphological traits (e.g. Blouw & Hagen 1984; Hauser, Harr & Schlötterer 2001; Hare &  
53 Elle 2004; Ruxton, Sherratt & Speed 2004; Wise, Yi & Abrahamson 2009; Moore *et al.* 2014).  
54 Polymorphism in defence levels within a prey or host species has been interpreted as a type  
55 of Batesian mimicry, the so-called “automimicry” (e.g. Brower 1960; Augner & Bernays  
56 1998; Ruxton, Sherratt & Speed 2004; Svennungsen & Holen 2007; Moore *et al.* 2014). One  
57 potential mechanism maintaining dimorphism in defence levels is the negative  
58 frequency-dependent selection (also known as apostatic selection) (Sherratt & Harvey 1993;  
59 Ruxton, Sherratt & Speed 2004). If this type of selection occurs, the rarer morphs have higher  
60 fitness compared to the abundant ones and consequently increase in frequency over time,  
61 allowing multiple morphs to coexist within a population. Thus, evolutionary ecologists have  
62 often asked how negative frequency-dependent selection may be a consequence of consumer  
63 response to polymorphism in defence levels of resources (e.g. Matthews 1977; Ruxton,  
64 Sherratt & Speed 2004; Svennungsen & Holen 2007).

65 Optimal foraging behaviour of consumers has been proposed as a mechanism that  
66 can generate negative frequency-dependent selection (e.g. Murdoch 1969; Matthews 1977;  
67 Abrams 1982; Holt 1983). For example, the optimal diet choice (ODC) theory predicts that  
68 the density of preferred resource alters the optimal level of preference to suboptimal ones so  
69 that consumers maximize their energy gain (MacArthur & Pianka 1966; Charnov 1976).  
70 Because such a change in preference increases the consumption rate for suboptimal resource  
71 as the density of preferred resource reduces, the consumption following ODC potentially  
72 drives the negative frequency-dependent selection on resource polymorphism (Abrams 1982;

73 Holt 1983). Indeed, several experimental studies have shown that such frequency-dependent  
74 consumption results in negative frequency-dependent selection between multiple morphs in  
75 animal prey (e.g. Brower 1960; Skelhorn & Rowe 2005; Fitzpatrick, Shook & Izally 2009)  
76 and consequently maintains the polymorphism in an experimental prey population (Bond &  
77 Kamil 1998). However, there is still limited evidence of the contribution of ODC to the  
78 maintenance of defence polymorphism in a natural population.

79         In plant–herbivore interactions, the risk of herbivory in individual plants depends not  
80 only on plants’ own phenotypes but also on those of the neighbouring plants (e.g. Barbosa *et*  
81 *al.* 2009; Wise, Yi & Abrahamson 2009; Sato & Kudoh 2016; Verschut *et al.* 2016). This  
82 phenomenon has been called “associational effects” (Barbosa *et al.* 2009; Underwood, Inouye  
83 & Hambäck 2014) and may influence plant’s coexistence through frequency-dependent  
84 herbivory (Underwood, Inouye & Hambäck 2014). To date, many empirical studies have  
85 suggested that herbivore behaviour mediates such associational effects between differentially  
86 defended plants (e.g. Hjältén, Danell, & Lundberg 1993; Bergvall & Leimar 2005; Rautio *et*  
87 *al.* 2012; Sato & Kudoh 2016; Verschut *et al.* 2016). For example, if herbivores choose  
88 among individual plants growing in a close proximity, this food preference could lead to an  
89 increased benefit of the defence, namely associational resistance, for unpalatable plants  
90 within patches (Bergvall & Leimar 2005; Sato & Kudoh 2016; Verschut *et al.* 2016; Hahn &  
91 Orrock 2016). If herbivores avoid unpalatable plants and prefer to palatable plants in a  
92 neighbourhood, associational susceptibility for palatable plants may occur at the same time  
93 within a patch (Verschut *et al.* 2016; Hahn & Orrock 2016). Theoretical studies also suggest  
94 that such a food choice by herbivores may lead to the associational effects and the  
95 coexistence of defended and undefended plants (Holt & Kotler 1987; Ishii & Crawley 2011;  
96 Hambäck *et al.* 2014). Little is known, however, about the role of foraging behaviour of

97 herbivores in associational effects and the maintenance of defence polymorphism.

98           Several plant species of the genus *Arabidopsis* exhibit dimorphism in trichome  
99 production within populations, having both trichome-producing (hereafter, hairy) and  
100 trichomeless (hereafter, glabrous) individuals (Hauser, Harr & Schlötterer 2001; Kawagoe *et*  
101 *al.* 2011). *Arabidopsis* trichomes confer resistance to leaf chewing herbivores (Mauricio  
102 1998; Sletvold *et al.* 2010; Sato *et al.* 2014; Sato & Kudoh 2016) but impose a fitness cost on  
103 plants (Mauricio 1998; Sletvold *et al.* 2010; Kawagoe *et al.* 2011). In *A. halleri* (L.) O’Kane  
104 & Al-Shehbaz subsp. *gemmifera* (Matsum.) O’Kane & Al-Shehbaz [Brassicaceae], the  
105 brassica leaf beetle, *Phaedon brassicae* Baly [Coleoptera: Chrysomelidae], preferred  
106 glabrous plants when hairy ones were rare and thereby mediated a frequency-dependent  
107 damage between hairy and glabrous plants in the field (Sato *et al.* 2014; Sato & Kudoh  
108 2017a). Our laboratory experiment also found that hairy plants incurred a growth cost of  
109 defence and the growth rate of each morph was negatively correlated with its own frequency  
110 under the defence–growth trade-off (Sato & Kudoh 2016). These findings suggest that the  
111 leaf beetle drives associational effects and consequently causes a frequency-dependent  
112 selection (Sato & Kudoh 2017a), but this hypothesis has not been tested explicitly.

113           In this study, we combined theoretical models and empirical data to test the  
114 hypothesis that foraging behaviours of *P. brassicae* contribute to the maintenance of trichome  
115 dimorphism in natural *A. halleri* populations. Specifically, the following three questions were  
116 addressed in this study: (1) Does optimal diet choice (ODC) account for the observed damage  
117 by leaf beetles in hairy and glabrous individuals? (2) Can ODC explain the observed patch  
118 dynamics of hairy and glabrous plants in the field? (3) Does ODC contribute to the  
119 coexistence of hairy and glabrous morphs via negative frequency-dependent selection?

120

## 121 MATERIALS AND METHODS

122

### 123 Study organisms

124 *Arabidopsis halleri* is a self-incompatible perennial herb distributed across Japan and the  
125 Russian Far East. Hairy individuals of this subspecies produce non-glandular trichomes on  
126 their leaf and stem surfaces (Fig. 1a), whereas glabrous plants have no trichomes except on  
127 leaf margins (Fig. 1b). The hairy and glabrous phenotypes are associated with allelic  
128 variations in a single gene *GL1* (Kawagoe *et al.* 2011) for which glabrousness is considered  
129 recessive. Plants have no specialized organs for long-distance seed dispersal and produce  
130 clonal rosettes after flowering (Fig. 1d). Our field survey was conducted in a natural *A.*  
131 *halleri* population in central Japan (Taka-cho, Hyogo; 35°06'N, 134°56'E; Sato *et al.* 2014).  
132 Thousands of *A. halleri* plants occur in fragmented habitats along a creek, and no  
133 Brassicaceae species other than the study species inhabits the field site. *Phaedon brassicae* is  
134 abundant in the flowering season and impacts plant fecundity by damaging the flowering  
135 stems (Kawagoe & Kudoh 2010).

136 *Phaedon brassicae* is a crucifer-feeding agricultural pest distributed across Asia  
137 (Ôtake & Funaki 1958; Wang *et al.* 2007). The beetle reaches maturity around 3 weeks after  
138 hatching (Wang *et al.* 2007). Adults are flightless and access their host plants by walking  
139 (Ôtake & Funaki 1958) (Fig. 1c), and larvae develop on individual plants on which they  
140 hatch (Ôtake & Funaki 1958). Thus, adults select their host plants not among but within plant  
141 patches, and the damage to individual plants is attributable to host choice by adults during  
142 oviposition.

143

### 144 Leaf damage

145 We first focused on the foraging behaviour of the walking beetle *P. brassicae* in order to  
146 explain the pattern of leaf damage in hairy and glabrous plants. Individual *A. halleri* plants  
147 are spatially aggregated in the field; hereafter, this pattern of aggregation is denoted  
148 “patches”. The diameter of each plant patch was less than 1 m at the field site (Sato *et al.*  
149 2014). At this patch scale, adult beetles walk freely among individual plants of *A. halleri* and  
150 feed on them. However, since *P. brassicae* are flightless, the neighbouring plant patches are  
151 far more distant (mean  $\pm$  SD = 6.1  $\pm$  3.9 m,  $n$  = 48 patches) than the neighbouring plant  
152 individuals (mean  $\pm$  SD = 9.0  $\pm$  5.7 cm,  $n$  = 232 plants). Besides, the plant density within a  
153 patch does not depend on the patch size as the average distance between neighbouring plants  
154 was not significantly correlated with the patch diameter (cm) ( $r$  = -0.17,  $P$  = 0.25,  $n$  = 46  
155 patches). These facts lead us to assume that interpatch movements are much more costly for *P.*  
156 *brassicae* than the intrapatch movements and rarely happen during their host choice; thus, we  
157 focused on the optimization of host plant choice by *P. brassicae* at individual level within  
158 patches.

159 We applied the optimal diet choice (ODC) theory (MacArthur & Pianka 1966;  
160 Charnov 1976) to model the behavioural response by which *P. brassicae* optimize their  
161 foraging depending on the number of hairy and glabrous plants within a patch. The  
162 parameters of this ODC model were estimated using the laboratory data on leaf damage in  
163 hairy and glabrous plants (Sato & Kudoh 2016) and implemented to predict the patterns of  
164 field data on leaf damage (Sato *et al.* 2014).

165

166 **Theoretical model.** We consider a plant population to be composed of spatially  
167 isolated patches in which hairy and glabrous plants may co-occur. Herbivores stroll among  
168 individual plants within a patch and optimize their foraging behaviour. Because the distance

169 between neighbouring *A. halleri* plants is independent of the patch size, we assume that the  
 170 herbivore encounters any plant individual within the patch at a constant rate  $P$ . Thus, the  
 171 encounter rates for glabrous and hairy plants are represented as  $PN_g/(N_g+N_h)$  and  
 172  $PN_h/(N_g+N_h)$ , respectively, where  $N_g$  denotes the number of glabrous and  $N_h$  the number of  
 173 hairy plants within the patch. We represent the handling time of glabrous and hairy plants for  
 174 herbivores as  $H_g$  and  $H_h$  and their energy intake as  $E_g$  and  $E_h$ , respectively. We assumed that  
 175 for herbivores glabrous plants are a more profitable resource compared to hairy plants, i.e.  
 176  $E_g/H_g > E_h/H_h$ . According to the ODC model (Charnov 1976), feeding on both glabrous and  
 177 hairy plants is optimal for herbivores when

$$178 \quad \frac{E_h}{H_h} > \frac{\frac{PN_g}{N_h + N_g} E_g}{1 + \frac{PN_g}{N_h + N_g} H_g} \quad \text{Eq. (1)}$$

179 Otherwise, feeding only on glabrous plants gives herbivores better energy acquisition  
 180 than feeding on both. Solving Eq. (1) by using the frequency of hairy plants  $f = N_h/(N_h+N_g)$ ,  
 181 we obtain the threshold frequency of hairy plants at which herbivores should switch their  
 182 foraging tactics  $f^*$ , i.e.

$$183 \quad f^* = 1 - \frac{se}{h - e}, \quad \text{Eq. (2)}$$

184 where  $e = E_h/E_g$ ,  $h = H_h/H_g$ , and  $s = 1/PH_g$ .

185 Although the original ODC theory predicts the abrupt change of preferences to a  
 186 suboptimal resource at  $f = f^*$ , in nature such a preference will gradually change with the  
 187 frequency of the suboptimal resource (Stephens & Krebs 1986) because of the incorrect  
 188 estimation of the frequency of suboptimal plant or the limited knowledge of the environment  
 189 (McNamara & Houston 1987; Křivan 2010). Thus, we assumed that the probability of

190 feeding on hairy plants  $D(f)$  gradually changes with the frequency of hairy plants  $f$ . Following  
 191 the formula of McNamara and Houston (1987),

$$192 \quad D(f) = \frac{1}{1 + \exp[-\alpha(f - f^*)]}, \quad \text{Eq. (3)}$$

193 where  $\alpha$  denotes the accuracy of herbivore response; at very large  $\alpha$  the  $D(f)$  values are the  
 194 same as those predicted by the original ODC model (i.e.  $D(f) = 0$  when  $f < f^*$ ,  $D(f) = 1$  when  $f$   
 195  $\geq f^*$ ). Note that the probability of feeding on glabrous plants is always one, because the partial  
 196 preference for glabrous plants always reduces the total energy acquisition.

197 When herbivores feed on plants as the result of partial preference to hairy plants  $D(f)$ ,  
 198 the damage by herbivory to glabrous and hairy plants are

$$199 \quad \frac{\varepsilon}{s + (1 - f) + fhD(f)} \frac{M(N_g, N_h)}{N_g + N_h} \quad \text{and} \quad \text{Eq. (4a)}$$

$$200 \quad \frac{\varepsilon D(f)}{s + (1 - f) + fhD(f)} \frac{M(N_g, N_h)}{N_g + N_h}, \text{ respectively,} \quad \text{Eq. (4b)}$$

201 where  $\varepsilon$  is the coefficient of damage per attack and  $M(N_g, N_h)$  is the number of herbivores  
 202 within the patch (see Appendix S1 in Supporting Information for the derivation). Although  
 203 the functional shape of  $M(N_g, N_h)$  has often been discussed (cf. Hambäck *et al.* 2014), the  
 204 damage to *A. halleri* was proportional to the number of plants in a patch in our study site  
 205 (Appendix S2); therefore, in the following analysis we assumed the linear relationship, i.e.  
 206  $M(N_g, N_h) = m(N_g + N_h)$  (but see Appendix S2 for non-linear analyses). Then, the damages to  
 207 a glabrous and hairy plant are

$$208 \quad \frac{v}{s + (1 - f) + fhD(f)} \quad \text{and} \quad \text{Eq. (5a)}$$

$$209 \quad \frac{vD(f)}{s + (1 - f) + fhD(f)}, \text{ respectively,} \quad \text{Eq. (5b)}$$

210 where  $v = \varepsilon m$ .

211

212 **Data.** Two datasets were used to predict herbivory by *P. brassicae*. The laboratory  
213 experimental data provided the extent of leaf damages (evaluated as a proportion of lost leaf  
214 area) by adult *P. brassicae* under two ratios of hairy to glabrous individuals (3:1 and 1:3)  
215 (Sato & Kudoh 2016). The field observational data provided the extent of leaf damage  
216 (evaluated as the proportion of leaf area lost to herbivory; scored from 0 to 1.0 at 0.1  
217 increments) in hairy and glabrous plants in a set of circular monitoring plots (1 m in  
218 diameter) (Sato *et al.* 2014). The details of the field surveys and experiments are described in  
219 previous publications (Sato *et al.* 2014; Sato & Kudoh 2016). The dataset used in the present  
220 study is available at the Dryad Digital Repository (Sato, Ito & Kudoh 2017).

221

222 **Statistical analysis.** We first estimated the model parameters of ODC ( $e$ ,  $h$ ,  $s$ , and  $\alpha$ )  
223 from the laboratory experimental data on leaf damage (Sato & Kudoh 2016). The leaf damage  
224 to individual plants was fitted by a least-square method. For the parameter estimation, we  
225 used the ‘optim’ function implemented in R version 3.2.0 (R Core Team 2015). The initial  
226 parameters were set at  $e = h = s = \alpha = 1.0$ . We first applied the Nelder-Mead method to avoid  
227 local optima, and then used the quasi-Newton method (BFGS method in R) to calibrate the  
228 parameters. Biases in these parameters were estimated using 95% percentiles of 10,000  
229 bootstrap samplings with replacement of the leaf damage data in individual plants.

230 To validate the parameters estimated from the laboratory data, we then compared the  
231 patterns of leaf damage in hairy and glabrous plants between the model prediction and field  
232 data (Sato *et al.* 2014). Given that the herbivore abundance and spatial scales differed  
233 between the field and laboratory, we scaled the model prediction to the level of field damage

234 as: Field damage =  $\beta \times$  Damage predicted by the ODC model (using the ‘nls’ function in R).

235

### 236 **Plant demography**

237 Because of the impact of herbivory on plant fecundity and/or mortality, foraging behaviour of

238 *P. brassicae* may affect the demographic dynamics of plants via negative

239 frequency-dependent selection between hairy and glabrous plants. The demography of

240 herbivores in each patch may be translated into herbivory pressure, which in turn influences

241 plant demography. For example, a better energy acquisition will enhance population growth

242 of herbivores, resulting in higher herbivory pressure in the next year. However, our field data

243 showed that the past leaf damage had a negligible influence on the current leaf damage

244 (Appendix S2), and therefore, we focused on the demography of hairy and glabrous *A. halleri*

245 and ignored the population dynamics of *P. brassicae*.

246 We developed a plant demography model where the plant mortality and/or fecundity

247 were affected by the damage derived from the ODC model, Eq. (5a) and (5b). The parameters

248 of the plant demography model were estimated by fitting the model to the field data on the

249 annual change in the number of hairy and glabrous plants in a set of patches. We then used

250 the estimated parameters to test how ODC by *P. brassicae* contributes to the coexistence of

251 hairy and glabrous plants in natural *A. halleri* populations.

252

253 ***Theoretical model.*** We considered that the field demography processes of plants

254 were characterized by two sequential events: death and recruitment. In the death event, some

255 of the plants die and thereby the number of plants in a patch decreases. We assumed that the

256 mortality of glabrous and hairy plants increased linearly with the damage caused by herbivory,

257 i.e.

258  $m_c + m_d \frac{v}{s + (1-f) + fhD(f)}$  and Eq. (6a)

259  $m_c + m_d \frac{vD(f)}{s + (1-f) + fhD(f)}$ , respectively, Eq. (6b)

260 where  $m_c$  is the constant intrinsic mortality, and  $m_d$  is the coefficient of additional mortality  
 261 due to the damage by herbivory. The total number of dead plants is represented as a  
 262 binominal distribution with the probability given by Eq. (6a) and (6b) (see Appendix S3 for  
 263 details).

264 In the recruitment event, new plants are recruited in each patch and thereby the  
 265 number of plants in the patch increases. We assumed that the fecundity (i.e. the number of  
 266 seeds or clones) linearly decreased with damage (Eq. (5a) and (5b)) and the cost of trichome  
 267 production  $c$ . Then, the total fecundity of glabrous and hairy plants in a focal patch are

268  $R \left[ 1 - \frac{v}{s + (1-f) + fhD(f)} \right] n_g$  and Eq. (7a)

269  $R \left[ 1 - \frac{vD(f)}{s + (1-f) + fhD(f)} - c \right] n_h$ , respectively, Eq. (7b)

270 where  $R$  is the potential number of offspring per capita, and  $n_g$  and  $n_h$  are the number of  
 271 glabrous and hairy plants within the patch, respectively. In *A. halleri*, the plants produce  
 272 clonal rosettes and seeds are dispersed by gravity. Thus, we assumed that a fraction of  
 273 produced offspring is dropped within the same patch, while the others reach different patches  
 274 that are randomly selected from the population. When we represent the former and the latter  
 275 fraction as  $1-d$  and  $d$ , respectively, the number of offspring of glabrous and hairy plants  
 276 reaching a focal patch are

277  $d\tilde{R}_g + (1-d)R \left[ 1 - \frac{v}{s + (1-f) + fhD(f)} \right] n_g$  and Eq. (8a)

278 
$$d\tilde{R}_h + (1-d)R \left[ 1 - \frac{vD(f)}{s + (1-f) + fhD(f)} - c \right] n_h$$
, respectively, Eq. (8b)

279 where  $\tilde{R}_g$  is the mean value of Eq. (7a) and  $\tilde{R}_h$  is the mean value of Eq. (7b) in the population.  
280 We assumed that all the offspring that reached the focal patch will establish and mature in  
281 that patch (However, our results were unchanged even when we incorporated the effect of  
282 patch size on the invasion difficulty; see Appendix S4.). Although the distribution of the  
283 number of newly established plants is uncertain, we approximate the probability distribution  
284 of the number of established individuals by a Poisson distribution with the mean given by Eq.  
285 (8a) and (8b).

286 In *A. halleri*, individual plants reproduce once a year in spring (Kawagoe & Kudoh  
287 2010), while the death event occurs throughout the year. Our field observations were  
288 conducted at the end of reproductive season of each year (mid-May; see the next subsection).  
289 Thus, the annual life cycle of *A. halleri* can be represented by a single recruitment event  
290 followed by a single death event. Consequently, we can quantify the occurrence probability  
291 of annual demographic changes by summing up the probability of all possible combinations  
292 for the number of dead and recruited plants, which follow a binominal distribution (with the  
293 probability as defined by Eq. (6a) and (6b)) and a Poisson distribution (with the mean defined  
294 by Eq. (8a) and (8b)), respectively (see Appendix S3 for details of the derivation).

295

296 **Data.** Once a year from 2013 to 2016, we randomly selected 80 plant patches and set  
297 circular monitoring plots to count the number of all hairy and glabrous plants in the plots.  
298 Given that the number of plants within the circular area approached a plateau at 1-m diameter  
299 in this site (Sato *et al.* 2014), the diameter of circular plots was set at 1 m to monitor patch  
300 size dynamics. The survey was conducted in the late flowering season (mid-May). Leaf

301 damages during this study period fully reflected the level of herbivory on individual plants as  
302 it occurred immediately after the spring outbreak of *P. brassicae*. We surveyed ca. 80 plots  
303 per year and obtained 243 measurements of their yearly dynamics. Given the clonality of *A.*  
304 *halleri*, a plant with no vegetative connection with others was designated as an individual in  
305 this survey.

306         Additionally, we used laboratory data on the biomass (mg) of hairy and glabrous  
307 plants to compare the estimated cost of defence  $c$  with our previous evidence on the growth  
308 cost of trichomes (Sato & Kudoh 2016). Potted plants were cultivated for 6 months in an  
309 indoor space without herbivory. The intrinsic growth cost for hairy plants was calculated as  
310  $[\ln(\text{median glabrous biomass}) - \ln(\text{median hairy biomass})] / \ln(\text{median glabrous biomass})$ .  
311 The details regarding the cultivation are described in Sato and Kudoh (2016). The dataset  
312 used in the present study is available at the Dryad Digital Repository (Sato, Ito & Kudoh  
313 2017).

314

315         **Statistical analysis.** Using the estimated parameters of the ODC model ( $e$ ,  $h$ ,  $s$ , and  
316  $\alpha$ ), we then estimated the six parameters ( $v$ ,  $R$ ,  $c$ ,  $d$ ,  $m_c$ , and  $m_d$ ) of the plant demography  
317 model. The field patch data on the number of hairy and glabrous plants observed from 2013  
318 to 2015 were used to quantify the likelihood of the observed field dataset pertaining to annual  
319 patch dynamics in our plant demography model (see Appendix S3 for derivation). To increase  
320 the log-likelihood of observed data, we ran eight independent chains of Markov chain Monte  
321 Carlo (MCMC) with  $10^6$  iterations,  $10^3$  thinning interval, and  $10^5$  burn-in period, starting  
322 from the following initial parameters:  $v = 0.0$ ,  $R = 1.0$ ,  $c = 0.0$ ,  $d = 0.5$ ,  $m_c = 0.5$ , and  $m_d =$   
323  $0.01$ . The mortality due to herbivory  $m_d$  was estimated at an exponential scale to examine a  
324 range of positive values. Proposal parameters were generated following a normal distribution

325  $N(\mu_t, \sigma^2)$ , where  $\mu_t$  denotes the parameter value at the current iteration, and  $\sigma$  is set at 0.25 for  
326  $v$  and  $R$  and at 0.025 for  $c$ ,  $d$ ,  $m_c$ , and  $m_d$ . These proposals were accepted/rejected following  
327 the Metropolis algorithm (Hastings 1970). The convergence of MCMCs was assessed  
328 by  $\hat{R}$  statistic at  $< 1.1$  (Plummer *et al.* 2006). If parameters were estimated to nearly zero,  
329 the  $\hat{R}$  statistic was calculated after excluding such ineffective parameters. The present  
330 modelling and parameter estimation were conducted using the Rcpp (Dirk & Francois 2011),  
331 BH (Dirk, Emerson & Kane 2015), coda (Plummer *et al.* 2006) package, and Rtools version  
332 3.3.0.1958 (available from: <https://cran.r-project.org/bin/windows/Rtools/>). The R code is  
333 available at the Dryad Digital Repository (Sato, Ito & Kudoh 2017).

334

## 335 **RESULTS**

336

### 337 **Prediction of leaf damage patterns**

338 We first estimated the parameters of our ODC model by fitting the predicted damage, Eq. (5a)  
339 and (5b), to the laboratory data. Glabrous plants were a more profitable resource for *P.*  
340 *brassicae* than hairy plants as shown by the greater handling time ( $h = 1.82$ ; Table 1a) and  
341 lower energy intake ( $e = 0.58$ ; Table 1a) of hairy plants. Given the set of the estimated  
342 handling time, energy intake, searching time, and response accuracy in the laboratory (Table  
343 1a), our ODC model predicted that *P. brassicae* avoided hairy plants when hairy plants were  
344 rare, but fed on both hairy and glabrous plants when hairy ones were abundant (solid lines  
345 and circles in Fig. 2a, b). In other words, the defensive role of producing hairs is effective  
346 when the frequency of glabrous plants is increased, whereas glabrous plants receive weak  
347 effects from neighbours. This result shows that the ODC by *P. brassicae* causes the  
348 associational effects.

349 Our ODC model with the estimated parameters (Table 1a) provided a comparable  
350 pattern with the observed trends in the field, as the intervals of prediction overlapped between  
351 the model (solid lines in Fig. 2a, b) and field data (dashed lines in Fig. 2a, b) on leaf damages  
352 in the two morphs. Hairy plants were less damaged when they were rare, whereas the damage  
353 to glabrous plants did not depend on the frequency of the two morphs in the field (dashed  
354 lines and pale plots in Fig. 2a, b). These results indicate that the ODC by *P. brassicae*  
355 accounts for the pattern of leaf damage to hairy and glabrous plants.

356

### 357 **Prediction of plant demography**

358 Based on the estimated parameters of the ODC model (Table 1a), we next examined the sets  
359 of six parameters of the plant demography model that increase the likelihood of observed  
360 field data (Table 1b). The herbivory pressure  $\nu$ , cost of defence  $c$ , interpatch dispersal  $d$ , and  
361 intrinsic mortality  $m_c$  were involved in the field demography of hairy and glabrous plants,  
362 whereas the mortality due to herbivory  $m_d$  was negligible at nearly zero (Table 1b). The  
363 growth cost for hairy plants directly compiled from the laboratory biomass data showed a  
364 smaller but comparable level of the defence cost (empirical  $c = 0.09$  [0.02–0.13], bootstrap  
365 median with 95% confidence interval [CI]) with the estimated cost  $c$  ( $c = 0.22$  [0.15–0.24],  
366 median with 95% CI; Table 1b). Approximately 10% of the recruitment process was  
367 attributable to the interpatch dispersal ( $d = 0.10$  [0.08–0.13]; Table 1b). Convergence of  
368 MCMCs was confirmed by  $\hat{R}$  statistic ( $\hat{R} = 1.015$ ).

369 Then, we tested the validation of our estimation by forecasting the test data. Using  
370 the parameters estimated from the data obtained in the first three years (2013 to 2015), we  
371 numerically simulated plant demography for 2015 to 2016 and then compared the predicted  
372 dynamics with the morph-frequency and patch size observed in 2016. The probability density

373 of the frequency of hairy plants in a patch was comparable with that observed in 2016 (Fig.  
374 2c). The number of *A. halleri* plants observed in 2016 ranged within those predicted by the  
375 model (Fig. 2d). Although we assumed ODC by *P. brassicae*, the observed demography  
376 might be predicted without ODC. Therefore, we estimated the model parameters assuming  
377 the absence of ODC, i.e. no difference between glabrous and hairy plants for herbivores ( $h =$   
378  $e = 1$ ). This model selection showed that the model without ODC was less fitted to the  
379 observed demography than that with ODC (difference of the deviance information criterion,  
380  $\Delta\text{DIC} = 9.95$ ; see also Appendix S5). These results indicate that the morph-frequency and  
381 patch size dynamics are predictable by the plant demography model incorporating ODC.

382 We further assessed whether the estimated model showed a similar morph-frequency  
383 as observed in the natural population. The frequency of hairy plants at the equilibrium state  
384 was derived by analysing the condition under which fitness of the two morphs becomes equal  
385 (by solving Eq. (7a) and (7b); see Appendix S6 for derivation). We analysed the equilibrium  
386 frequency and its confidence intervals using the parameter sets sampled from MCMCs. These  
387 parameter sets predicted the intermediate frequency of hairy plants (predicted  $f = 0.53$   
388  $[0.45\text{--}0.62]$ , median  $[95\% \text{ CI}]$ ), and this interval of predicted frequency was overlapped with  
389 the observed frequency of hairy plants in the natural population (observed  $f = 0.52$   
390  $[0.47\text{--}0.58]$  estimated by 10,000 bootstrap replicates on plant patches surveyed in 2016).  
391 Thus, the estimated model provides quantitative prediction of the observed frequency in  
392 natural population.

393

### 394 **Coexistence of hairy and glabrous plants**

395 To test whether the model with estimated parameters (Table 1) predicts a negative  
396 frequency-dependent selection, we asked (1) whether rarer morphs have higher fitness than

397 abundant ones and (2) whether frequencies of rarer morphs increase over time. First, we  
398 calculated the relative fitness of hairy and glabrous plants with respect to the frequency of  
399 hairy plants in the population (Fig. 3a). The model predicts that relative fitness of one morph  
400 increases as it becomes relatively rare (Fig. 3a), showing negative frequency-dependent  
401 selection between the two morphs. Second, because the result based on the relative fitness  
402 does not include the effect of patch structure at the population scale, we performed numerical  
403 simulations to confirm negative frequency-dependent selection at such a population scale. We  
404 constructed a virtual plant population whose patch size followed the Poisson distribution with  
405 a mean patch size observed in the natural population ( $N_g + N_h = 10.03$ ) and simulated the  
406 patch size dynamics by applying the model with the estimated parameters (Table 1). The  
407 simulated dynamics showed that the frequency of hairy plants at the population scale  
408 approached the equilibrium frequency over time (blue points in Fig. 3b) even when the  
409 meta-patch structure was taken into consideration. Contrarily, a numerical simulation without  
410 any effects of ODC (i.e.  $h = e = 1$ ) did not show the frequency-dependent selection between  
411 the two morphs (red points in Fig. 3b). These results indicate that ODC by leaf beetles  
412 promotes the maintenance of trichome dimorphism via negative frequency-dependent  
413 selection.

414 Finally, we analysed the conditions under which the herbivory pressure  $\nu$  and  
415 defence cost  $c$  allow hairy and glabrous plants to coexist within a population (Fig. 3c; see  
416 also Appendix S6 for derivation). The estimated range of herbivory pressure  $\nu$  and the  
417 defence cost  $c$  was included within the predicted region where hairy and glabrous plants  
418 coexist (Fig. 3c). This region for coexistence was broader than that for extinction of one  
419 morph. This analysis indicates that, in the presence of ODC by leaf beetles, hairy and  
420 glabrous plants likely coexist even if the herbivory pressure and cost of defence vary across a

421 wide range.

422

## 423 **DISCUSSION**

424

### 425 **Optimal forager promotes the maintenance of polymorphism**

426 How natural enemies govern prey diversity is an intriguing and long-standing question in  
427 trophic interactions (e.g. Brower 1960; Murdoch 1969; Ruxton, Sherratt & Speed 2004).

428 Although several studies to date have shown the importance of natural enemies for  
429 coexistence of multiple prey (or host) species (Ishii & Shimada 2012) or morphs (Bond &  
430 Kamil 1998) in the laboratory, quantitative evidence in natural populations remains limited.  
431 Here, we have shown that optimal diet choice (ODC) by herbivores is a crucial mechanism  
432 stabilizing the coexistence of hairy and glabrous plants in a natural population based on the  
433 following three results. First, the pattern of leaf damage to hairy and glabrous plants was  
434 explained by ODC by the leaf beetles. Second, the model incorporating ODC better predicted  
435 plant demography than the model without ODC. Third, the numerical analysis and simulation  
436 revealed that ODC by the leaf beetle has driven a negative frequency-dependent selection that  
437 maintains the dimorphism of hairy and glabrous plants. These results present one of few field  
438 examples that demonstrate the stabilizing role of natural enemies in defence polymorphism.

439         The prediction of ODC wherein consumers feed on suboptimal resource when  
440 preferred resource is rare has been supported for many species (Pyke, Pulliam & Charnov  
441 1977; Sih & Christensen 2001), especially those feeding on sessile prey (Sih & Christensen  
442 2001). This prediction is applicable to adult host choice and consequent larval performance in  
443 herbivorous insects (Jaenike 1978; Scheirs & Bruyn 2002). Hairy plants are considered  
444 suboptimal for *P. brassicae* since larvae grow better when they are fed glabrous leaves than

445 hairy leaves (Sato *et al.* 2014). Given that larvae of *P. brassicae* have no opportunity to  
446 actively choose host plants (Ôtake & Funaki 1958), plant damages are attributable to adult  
447 host choice followed by larval feeding. Although the proximate mechanisms by which adult  
448 beetles recognise hairy and glabrous plants have yet to be elucidated, ODC is a plausible  
449 mechanism underlying the pattern of plant damage.

450           Qualitatively speaking, the maintenance of defence polymorphism under  
451 herbivore-mediated interactions has often been discussed in the context of game theory that  
452 assumes the intrinsic cost and associational benefits of the defence among defended and  
453 undefended plants (Augner & Bernays 1998; Rautio *et al.* 2012). There is a growing body of  
454 evidence on the cost of physical and chemical defence against herbivores (e.g. Mauricio  
455 1998; Hare & Elle 2004; Sletvold *et al.* 2010). More importantly, recent studies on  
456 associational effects have shown that food preference by herbivores causes associational  
457 resistance for unpalatable plants and simultaneously leads to associational susceptibility for  
458 plants within a patch (Verschut *et al.* 2016; Hahn & Orrock 2016). In contrast, ODC by the  
459 leaf beetle *P. brassicae* predicts intrapatch associational resistance for hairy plants, but not  
460 associational susceptibility for glabrous plants. This is because the handling time on hairy  
461 plants is much longer than that on glabrous plants ( $h = 1.82$ ; Table 1a) and thereby the  
462 existence of hairy plants decreases the attack rate to glabrous plants. As discussed in the  
463 former paragraph, optimal foragers are expected to feed on unpalatable food only when  
464 palatable food becomes rare (MacArthur & Pianka 1966; Charnov 1976). In terms of ODC,  
465 our present study explains why only the associational resistance for unpalatable plants occur  
466 within a patch.

467           Remarkably, the coexistence of two morphs was widely predicted across the  
468 parameter region of the defence cost  $c$  or herbivory pressure  $h$ . For example, under the

469 estimated parameters, the coexistence can still be possible even if the defence reduces the  
470 reproductive success by almost 50% (Fig. 3c). Moreover, according to the estimated  
471 parameters (Table 1a), the preference for hairy plants changes very gradually with the  
472 frequency of the hairy plants, i.e. the probability of feeding on hairy plants  $D(f)$  is expected to  
473 be 0.43 and 0.90 when the patch is filled by glabrous plant ( $f = 0$ ) and hairy plant ( $f = 1$ ),  
474 respectively. Therefore, neither the subtle balance between cost and benefit of the defence nor  
475 the high accuracy of herbivore foraging is a necessary condition for the coexistence of two  
476 morphs. This line of analysis implies that the stabilizing role of ODC by herbivores in the  
477 maintenance of defence polymorphism may be widespread in plant–herbivore and other  
478 trophic interactions.

479

#### 480 **Disentangling species interaction under complex field environment**

481 Spatial heterogeneity within a single population is hypothesized to be important as plants are  
482 incapable of escaping from herbivores (Ishii & Crawley 2011; Hambäck *et al.* 2014).  
483 Considering a meta-patch structure and the intrapatch effects of herbivore foraging, we were  
484 able to evaluate the relative importance of interpatch dispersal and intrapatch herbivory in the  
485 morph-frequency dynamics. The result that showed that the intrapatch dispersal of plants was  
486 predominant compared to the interpatch dispersal (as indicated by the estimated proportion of  
487 interpatch dispersal,  $d = 0.10$ ) seems convincing, because *A. halleri* plants disperse their  
488 offspring near a maternal plant by clonal propagation or seed dispersal by gravity. Separating  
489 the plant life cycle into the two stages, we also uncovered the impact of herbivory on the  
490 recruitment but not on the death stage. This result agrees with the fact that *P. brassicae*  
491 become abundant in the recruitment season, decreasing plant fecundity (Kawagoe & Kudoh  
492 2010). Given that *A. halleri* individuals are rarely killed by infestation by *P. brassicae* alone

493 (only one dead out of 120 plants as reported by Sato & Kudoh 2016), it was conceivable that  
494 herbivory did not affect mortality.

495         Although our study found that foraging behaviour of *P. brassicae* contributes to the  
496 maintenance of polymorphism in *A. halleri*, this does not necessarily indicate the absence of  
497 other factors affecting the frequency of defended plants within a population. Co-occurrence  
498 of defended and undefended morphs might also be allowed by spatiotemporal variation in  
499 herbivory pressure and migration among populations (Hare & Elle 2004; Andrew *et al.* 2007;  
500 Sato & Kudoh 2017b). The frequencies of hairy and glabrous plants and the prevalent  
501 herbivore species indeed vary among *A. halleri* populations (Sato & Kudoh 2015; Sato &  
502 Kudoh 2017b). Notably, the present modelling approach enables us to quantify the stability of  
503 the morph frequency caused by ODC (Fig. 3b) or to perform a model selection that compares  
504 the predictability among multiple models (e.g. DICs). Although temporal dynamics between  
505 the current and past herbivory pressure were unclear in our 4-year survey (Appendix S2), this  
506 effect might be significant in long-term data. Further understanding of the relative importance  
507 of multiple factors responsible for the co-occurrence of defended and undefended morphs  
508 will be possible by analysing the extended model combined with the long-term demography  
509 data from multiple plant populations.

510

## 511 **Conclusion**

512 Our present findings suggest that adaptive foraging by natural enemies may play a more  
513 important role in stabilizing defence polymorphism in the wild than previously thought.  
514 Recent studies have begun to adopt a likelihood approach to detect the ongoing  
515 frequency-dependent selection from the time-series polymorphism dynamics (Rouzic *et al.*  
516 2015) or to test the mechanisms underlying the coexistence of plant genotypes (Miller &

517 Rudgers 2014). Although our present study focused on *A. halleri* and *P. brassicae*, this type  
518 of modelling may be applied to other systems. Several studies on plant–herbivore interaction  
519 suggest that scales of associational effects depend on spatial structure of herbivores and  
520 plants (Hjältén, Danell, & Lundberg 1993; Sato & Kudoh 2015; Verschut *et al.* 2016). Now  
521 that evidence for apparent interaction has been accumulated in various trophic interactions  
522 (see Ruxton, Sherratt & Speed 2004 for animals; Barbosa *et al.* 2009 for plants), joint  
523 approaches using optimality modelling and empirical data will enable us to address how  
524 behavioural basis of natural enemies impacts prey diversity across ecosystems.

525

#### 526 **AUTHOR CONTRIBUTIONS**

527 YS collected and analysed the data. KI developed the mathematical models. YS, KI, and HK  
528 conceived the study and wrote the paper.

529

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535

#### 536 **DATA ACCESSIBILITY**

537 Source codes and data deposited in the Dryad Digital Repository:

538 <http://dx.doi.org/10.5061/dryad.pn088> (Sato, Ito & Kudoh 2017)

539

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679

## 680 **SUPPORTING INFORMATION**

681 Additional supporting information may be found in the online version of this article.

682

683 Appendix S1 Derivation of the damage

684 Appendix S2 Total amount of herbivory

685 Appendix S3 Derivation of the likelihood

686 Appendix S4 Influence of patch size

687 Appendix S5 The importance of ODC

688 Appendix S6 Condition for the coexistence

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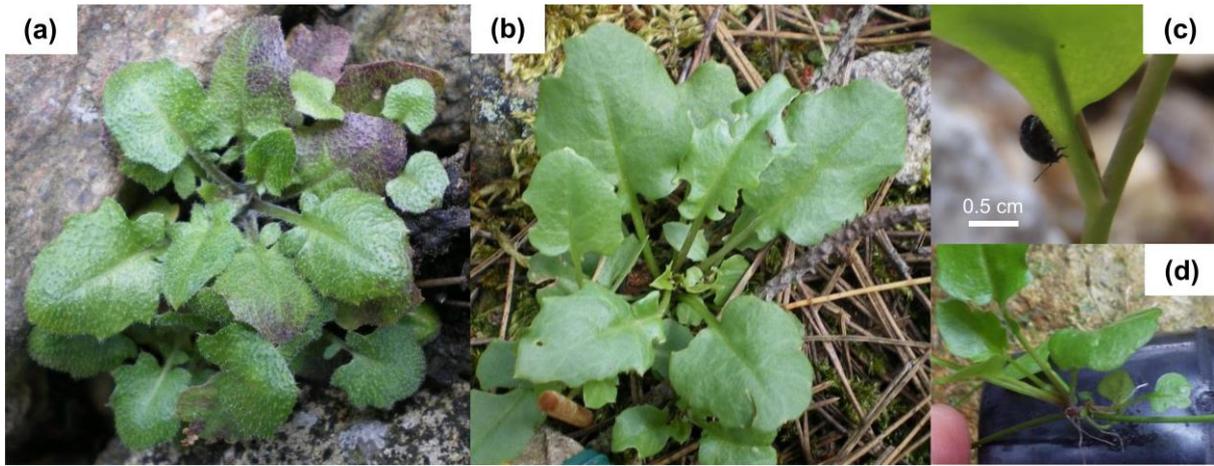
691 **Table 1** Estimated parameters of the herbivore behaviour and plant demography model.  
 692 (a) Least-square estimates for four parameters responsible for leaf damage to hairy and  
 693 glabrous plants in the laboratory. The optima estimated by the Nelder-Mead and  
 694 quasi-Newton method are shown with bootstrap confidence intervals (CIs).

Parameter	Description	Estimate	Bootstrap 95% CI	
			Lower	Upper
<i>h</i>	Handling time	1.81	1.39	2.58
<i>e</i>	Energy intake	0.58	0.48	1.28
<i>s</i>	Searching time	1.88	1.56	2.34
<i>α</i>	Response accuracy	2.52	1.58	3.05

695  
 696 (b) Markov Chain Monte Carlo estimates for six parameters determining plant demography  
 697 in the field. The median and 95% lower and upper percentiles are shown for parameter  
 698 distributions.

Parameter	Description	Percentiles		
		Median	2.5%	97.5%
<i>v</i>	Herbivory pressure	2.57	2.07	2.72
<i>R</i>	Intrinsic growth rate	12.87	5.61	21.84
<i>c</i>	Cost of defence	0.22	0.15	0.24
<i>d</i>	Proportion of interpatch dispersal	0.10	0.08	0.13
<i>m<sub>c</sub></i>	Intrinsic mortality	0.75	0.69	0.80
<i>m<sub>d</sub></i>	Mortality due to herbivory	<10 <sup>-8</sup>	<10 <sup>-36</sup>	0.03
---	<i>Log-Likelihood</i>	-730.3	-735.2	-728.4

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706 **Figure 1** Photographs of *Arabidopsis halleri* subsp. *gemmifera* and *Phaedon brassicae*: (a)

707 hairy plant; (b) glabrous plant; (c) adult beetle; and (d) clonal rosette producing roots.

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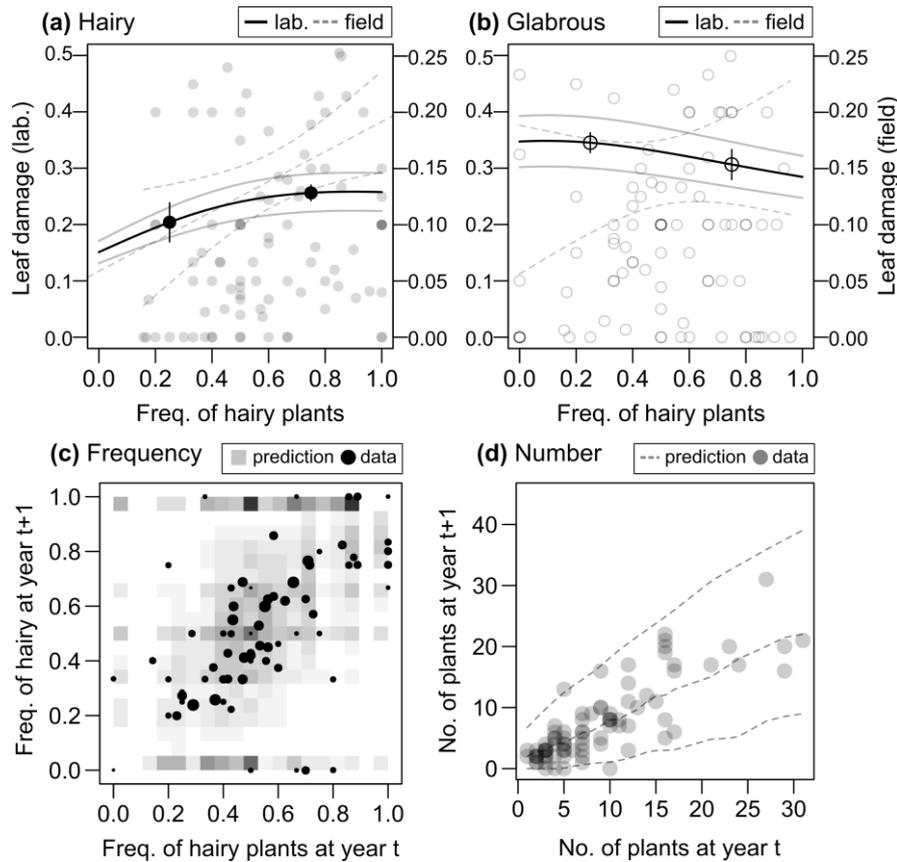
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724 **Figure 2** Prediction of leaf damage patterns and demography of hairy and glabrous plants.

725 Leaf damage (evaluated by proportion of the lost leaf area) to hairy (a) or glabrous (b) plants

726 predicted by the optimal diet choice (left axis) and observed in the field (right axis). Solid

727 curves and circles indicate the prediction ( $\pm 95\%$  CI) and average damage ( $\pm SE$ ) in the

728 laboratory (lab.), respectively. Dashed curves and pale circles show linear prediction ( $\pm 95\%$

729 CI) and average damage in the field. Prediction of the morph-frequency (c) and patch size (d)

730 dynamics observed from 2015 to 2016. (c) The plot size corresponds to the number of plants

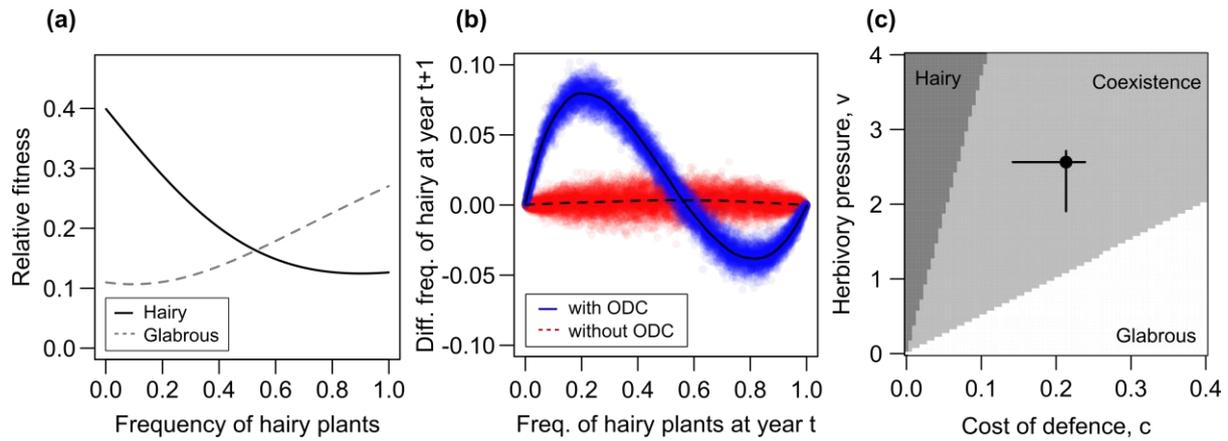
731 in a patch observed in 2015. The darkness of the squares represents the probability density of

732 the simulated frequency changes. (d) Dashed lines indicate the median and 95% prediction

733 intervals of the model simulation.

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737 **Figure 3** Negative frequency-dependent selection and the coexistence of hairy and glabrous

738 plants as shown by the estimated parameters. (a) Relative fitness between hairy (solid line)

739 and glabrous (dashed line) plants based on Eq. (S9a) and (S9b) in Appendix S6. (b)

740 Population level dynamics of the morph-frequency simulated by models with (blue plots;

741 solid line) or without (red plots; dashed line) the optimal diet choice (ODC). Trend lines are

742 added using a smooth spline method. A single point indicates a simulated plant population

743 consisting of 1,000 patches, and the simulation was repeated 100 times for each frequency.

744 (c) Condition for the coexistence of hairy and glabrous plants under combinations of the

745 herbivory pressure  $v$  and defence cost  $c$ . Circles and bars indicate the median and 95%

746 percentiles of the estimated  $v$  and  $c$ .

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755 **Appendix S1. Derivation of the damage by herbivory**

756 According to the optimal diet choice (ODC) model (Charnov 1976), the attack rate of a  
 757 herbivore on glabrous and hairy plants is

$$758 \quad \frac{P \frac{N_g}{N_g + N_h}}{1 + P \frac{N_g}{N_g + N_h} H_g + P \frac{N_h}{N_h + N_h} D(f) H_h} \quad \text{and} \quad \text{Eq. (S1a)}$$

$$759 \quad \frac{P \frac{N_h}{N_g + N_h} D(f)}{1 + P \frac{N_g}{N_g + N_h} H_g + P \frac{N_h}{N_h + N_h} D(f) H_h}, \text{ respectively.} \quad \text{Eq. (S1b)}$$

760 By using  $s, f,$  and  $h,$  we can rewrite Eq. (S1a) and (S1b) as

$$761 \quad \frac{1}{H_g} \frac{1-f}{s + (1-f) + fhD(f)} \quad \text{and} \quad \text{Eq. (S2a)}$$

$$762 \quad \frac{1}{H_g} \frac{fD(f)}{s + (1-f) + fhD(f)}, \text{ respectively.} \quad \text{Eq. (S2b)}$$

763 By dividing Eq. (S2a) and (S2b) by  $N_g$  and  $N_h,$  respectively, we obtain the frequency of  
 764 attacks by the focal herbivore on glabrous and hairy plants, i.e.

$$765 \quad \frac{1}{H_g} \frac{1}{s + (1-f) + fhD(f)} \frac{1}{N_g + N_h} \quad \text{and} \quad \text{Eq. (S3a)}$$

$$766 \quad \frac{1}{H_g} \frac{D(f)}{s + (1-f) + fhD(f)} \frac{1}{N_g + N_h}, \text{ respectively.} \quad \text{Eq. (S3b)}$$

767 In general, the number of herbivores depends on the patch size, i.e.  $N_g$  and  $N_h;$  therefore, we  
 768 represent the number of herbivores within the patch as  $M(N_g, N_h).$  By multiplying Eq. (S3a)  
 769 and (S3b) by  $M(N_g, N_h)$  and the level of damage caused per attack, we obtain the total  
 770 damage to glabrous and hairy plants, respectively. We defined  $\varepsilon$  as the quotient of damage per  
 771 attack divided by the handling time of glabrous plants  $H_g;$  then, we can represent the damages

772 to glabrous and hairy plants using Eq. (4a) and (4b), respectively.

773

## 774 **Appendix S2. Factors responsible for the total amount of herbivory in a patch**

775 The number of herbivores usually shows a non-linear response to the number of plants in a  
776 patch (e.g. a square-root response, Hambäck *et al.* 2014). If the mobility of herbivores is  
777 limited during their life cycle, the current number of herbivores might also depend on their  
778 past abundance or fecundity in a patch. In this section, we first investigated the relationship  
779 between the number of plants and their leaf damage, which reflects the amount of resource  
780 acquired for herbivores. We also examined the relative importance of the past abundance of  
781 herbivores and the frequency of hairy plants on the total amount of leaf damage. Finally, we  
782 ran the MCMC estimation assuming a square-root response of the number of herbivores to  
783 patch sizes and compared the results with those estimated by assuming a linear response of  
784 the number of herbivores to patch sizes. For this line of analyses, we collected the leaf  
785 damage data as we monitored the number of hairy and glabrous plants in the field site during  
786 the 4-year observations (described in the main text). We evaluated the proportion of the lost  
787 leaf area for all individual plants in each patch using the same procedure as that described by  
788 Sato and Kudoh (2016).

789 We first determined a relationship between the total amount of damage and the  
790 number of plants in a patch as:  $\text{Damage} = a \times N^b$ , where  $N$  is the number of plants. The nls  
791 function in R was used to estimate the parameters  $a$  and  $b$ . This non-linear regression showed  
792 that the scaling parameter did not differ from 1 ( $b = 1.11 \pm 0.17$  [ $\pm 95\%$  CI],  $t = 12.8$ ,  $P <$   
793  $10^{-16}$ ). The coefficient  $a$  was  $0.08 \pm 0.02$  [ $\pm 95\%$  CI;  $t = 3.96$ ,  $P < 0.001$ ] in the non-linear  
794 regression. This results support our basic model assuming a linear response of *P. brassicae* to  
795 the number of *A. halleri* plants in a patch.

796 We then examined the factors responsible for the total amount of damage in a current  
797 year. A multiple regression was applied because of the linearity between the total damage and  
798 the number of plants. The response variable was the total amount of leaf damage in a current  
799 year in a patch, and the explanatory variables were the current number of plants, current  
800 frequency of glabrous plants, and the total amount of leaf damage in the previous year. As a  
801 result, the current amount of damage was positively correlated with the current number of  
802 plants and the previous amount of leaf damage (coefficient  $\pm$  SE =  $0.10 \pm 0.01$  and  $0.15 \pm$   
803  $0.04$ ,  $t = 11.8$  and  $3.6$ ,  $P < 10^{-16}$  and  $< 0.001$ , respectively), but not with the current frequency  
804 of glabrous plants (coefficient  $\pm$  SE =  $0.004 \pm 0.21$ ,  $t = 0.02$ ,  $P = 0.98$ ). This result indicates a  
805 negligible effect of the morph-frequency on the amount of herbivory. Despite the statistical  
806 significance of the past leaf damage, the current number of plants contributed more to the  
807 current amount of damage ( $R^2 = 0.29$  and  $0.04$  for the current number and past damage,  
808 respectively). Temporal dynamics of herbivory was therefore unclear in the present field data  
809 on *A. halleri*.

810 To test how the assumption about the number of herbivores alters the fitting of our  
811 plant demography model to the field data, we additionally ran MCMC with the square-root  
812 number of plants (see “*Statistical analysis*” of “**Plant demography**” in the main text). This  
813 square-root response of herbivores has specifically been reported as a resource dilution effect  
814 on herbivory (Hambäck *et al.* 2014). The calculated log-likelihood was, however, smaller  
815 ( $-736.7$  [ $-741.1$  to  $-734.8$ ], median and 95% CI) than the MCMC with the non-transformed  
816 number of plants in a patch, thus assuming the square-root relationship between the number  
817 of herbivores and the number of plants impaired the fitting to the field data.

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819

820 **Appendix S3. Likelihood of the observed dynamics of a plant patch**

821 Hereafter, we refer to a patch where the number of glabrous and hairy plants is  $N_g$  and  $N_h$ ,  
822 respectively, as  $\{N_g, N_h\}$ . First, we consider the probability  $\text{Pr}_D$  that the patch  $\{N_g, N_h\}$   
823 becomes  $\{n_g, n_h\}$  after the death stage. If we assume that the death event of each plant occurs  
824 independently, the number of dead plants follows a binomial distribution whose probability is  
825 the mortality, as expressed in Eq. (6a) and (6b). Then, we can calculate the probability  $\text{Pr}_D$  by  
826 multiplying the two probability mass functions of the binominal distribution, i.e.

$$827 \quad \text{Pr}_D(\{n_g, n_h\}|\{N_g, N_h\}) = \binom{N_g}{n_g} \mu_g^{N_g - n_g} (1 - \mu_g)^{n_g} \binom{N_h}{n_h} \mu_h^{N_h - n_h} (1 - \mu_h)^{n_h},$$

828 Eq. (S4a)

829 where  $\mu_g$  and  $\mu_h$  are the mortality of glabrous and hairy plants, i.e. Eq. (6a) and (6b),  
830 respectively, and

$$831 \quad \binom{n}{k} = \frac{n!}{k!(n-k)!}. \quad \text{Eq. (S4b)}$$

832 Next, we focus on the probability  $\text{Pr}_R$  that a patch  $\{n_g, n_h\}$  becomes  $\{N'_g, N'_h\}$  after  
833 the recruitment stage. Here, we assume that the probability distribution of the number of  
834 established individuals follows a Poisson distribution with the mean number of glabrous ( $\lambda_g$ )  
835 and hairy plants ( $\lambda_h$ ) equal to Eq. (8a) and (8b), respectively. Therefore, the probability  $\text{Pr}_R$  is  
836 represented as

$$837 \quad \text{Pr}_R(\{N'_g, N'_h\}|\{n_g, n_h\}) = \frac{\lambda_g^{N'_g - n_g} e^{-\lambda_g}}{N'_g - n_g} \frac{\lambda_h^{N'_h - n_h} e^{-\lambda_h}}{N'_h - n_h} \quad \text{Eq. (S5)}$$

838 Summing up the probabilities of all possible outcomes of death and recruitment  
839 stages, we obtain the probability that the patch  $\{N_g, N_h\}$  becomes  $\{N'_g, N'_h\}$  at the next time  
840 step, i.e.

$$841 \quad \sum_{n_g=0}^{N_g} \sum_{n_h=0}^{N_h} \left[ \Pr_D(\{N_g - n_g, N_h - n_h\} | \{N_g, N_h\}) \Pr_R(\{N'_g, N'_h\} | \{N_g - n_g, N_h - n_h\}) \right]$$

842 Eq. (S6)

843 By using a certain parameter set, Eq. (S6) provides the probability that a given plant patch  
 844  $\{N_g, N_h\}$  turns into another state  $\{N'_g, N'_h\}$  during a year. Multiplying the probabilities over a  
 845 set of patches, we obtain the likelihood, i.e. a joint probability, to show how likely the  
 846 observed dataset for patch dynamics in the field is in the plant demography model consisting  
 847 of death (binomial error) and recruitment (Poisson error) events.

848

#### 849 **Appendix S4. The influence of patch size on invasion difficulty**

850 Our basic model assumed that all seeds or clones reached to a given patch can be established  
 851 and mature at the patch. However, because of the spatial or resource limitation of the patch,  
 852 the patch size might reduce the probability that seeds or clones successfully establish  
 853 themselves and mature in the focal patch. To investigate such a density effect, let us consider  
 854 a situation in which the probability of being established decreases linearly with the number of  
 855 mature plants at the focal patch, i.e. the established probability is  $1 - k(n_g + n_h)$ , where  $k$  is  
 856 the coefficient of the mature plant number effect. Then, the mean number of glabrous and  
 857 hairy plants established at a patch  $\{n_g, n_h\}$  is

$$858 \quad \lambda_g = \left(1 - k(n_h + n_g)\right) \left( d\tilde{R}_g + (1-d)R \left[ 1 - \frac{v}{s + (1-f) + fhD(f)} \right] n_g \right) \text{ and Eq. (S7a)}$$

$$859 \quad \lambda_h = \left(1 - k(n_h + n_g)\right) \left( d\tilde{R}_h + (1-d)R \left[ 1 - \frac{vD(f)}{s + (1-f) + fhD(f)} - c \right] n_h \right), \text{ Eq. (S7b)}$$

860 respectively.

861 We applied MCMCs to the extended model in addition to the six demographic

862 parameters ( $v$ ,  $R$ ,  $c$ ,  $d$ ,  $m_c$ , and  $m_d$ ). The parameter  $k$  was estimated as an exponential scale to  
863 examine the range of positive values. As described in the main text, we ran eight independent  
864 chains of  $10^6$  iterations of MCMCs with a  $10^5$  burn-in period and  $10^3$  thinning interval. The  
865 initial parameters of  $k$  and  $m_d$  were set to 0.01, and the same initial constraints, as shown in  
866 the main text, were applied to the remaining five parameters. According to the MCMC  
867 analysis, the effect of the mature plant  $k$  was estimated at nearly zero ( $k < 0.01$  at upper 95%  
868 CI). The estimated values of the other six parameters ( $v$ ,  $R$ ,  $c$ ,  $d$ ,  $m_c$ , and  $m_d$ ) and the  
869 log-likelihood were the same as those of the model without  $k$  up to the level of second  
870 significant figures. Thus, plant density had negligible effects on the recruitment process.

871

## 872 **Appendix S5. Importance of ODC in model predictions**

873 In this section, we investigated the effects of the defensive advantage of hairy plants, i.e. the  
874 relative energy intake  $e$  and the relative handling time  $h$ , on parameter estimations and model  
875 predictions. First, we focused on the parameter estimation of ODC ( $e$ ,  $h$ ,  $s$ , and  $\alpha$ ) from the  
876 leaf damage data obtained in the laboratory experiment. Although we estimated these  
877 parameters assuming that both energy intake and handling time were different between the  
878 herbivory of glabrous and hairy plants, either of them might be the same between the two  
879 plant morphs (i.e. the situation that  $e = 1$  or  $h = 1$ ). However, the estimated damage to hairy  
880 and glabrous plants were insufficiently fitted to the average damage estimated from the  
881 empirical data when  $e = 1$  or  $h = 1$  (Figure S1). These results indicate that incorporating both  
882 the increment of handling time and the decrement of energy intake is necessary to explain the  
883 observed pattern of leaf damage.

884           Next, to examine the effects of ODC on model predictions, we investigated the  
885 simulation model assuming no difference between glabrous and hairy plants in both energy

886 intake and handling time (i.e.  $e = h = 1$ ). In such a situation, the probability of feeding on  
 887 hairy plants  $D$  is always one, and the damage to glabrous and hairy plants, Eq. (5a) and (5b),  
 888 becomes a constant value  $v/(s + 1)$  regardless of the frequency of hairy plants  $f$ . Then, the  
 889 mortality of glabrous and hairy plants, Eq. (6a) and (6b), can be represented by a constant  
 890 value  $m$ . Similarly, the total number of offspring of hairy and glabrous plants, Eq. (8a) and  
 891 (8b), can be rewritten as

$$892 \quad d\tilde{R}_g + (1 - d)R'n_g \quad \text{and} \quad \text{Eq. (S8a)}$$

$$893 \quad d\tilde{R}_h + (1 - d)(R' - c')n_h, \quad \text{Eq. (S8b)}$$

894 respectively, where  $R' = R(1 - v/(s + 1))$  and  $c' = Rc$ .

895 We ran eight independent chains of  $10^6$  iterations of MCMCs with a  $10^5$  burn-in  
 896 period and  $10^3$  thinning interval to estimate the parameters  $R'$ ,  $c'$ ,  $d$ , and  $m$  (Table S1). We  
 897 used deviance information criteria (DICs; Spiegelhalter *et al.* 2002 *J. R. Stat. Soc. Series B*,  
 898 **64**, 583–639) to compare predictability of the models with and without ODC. The DICs were  
 899 calculated on the basis of the mean and variance of log-likelihoods from the MCMCs. The  
 900 model with ODC showed a smaller DIC (= 1474.2) than the model without ODC (= 1484.1),  
 901 indicating the importance of ODC in predicting the observed demography. The result that the  
 902 defence cost  $c$  was near to and overlapped with zero (Table S1a) showed that this cost needs  
 903 not be considered in the absence of ODC. Additionally, we estimated the model including the  
 904 carrying capacity based on a similar extension in Appendix S4. However, the inverse of  
 905 carrying capacity  $k$  exhibited nearly zero values and the results of the remaining parameters  
 906 were almost the same to those in the case without carrying capacity (Table S1b).

907

908 **Table S1** MCMC estimates for the model parameterised without ODC by herbivores ( $h = 1$   
 909 and  $e = 1$ ). The results of the estimates without **(a)** and with **(b)** the inverse of the carrying

910 capacity  $k$  are shown. The median with 95% lower and upper percentiles is shown for  
 911 parameter distributions.

**(a) Without carrying capacity**

Parameter	Description	Percentiles		
		Median	2.5%	97.5%
$R'$	Transformed growth rate	1.79	1.38	2.34
$c'$	Transformed cost of defence	-0.03	-0.41	0.35
$d$	Proportion of interpatch dispersal	0.11	0.08	0.14
$m$	Mortality	0.75	0.69	0.80
---	<i>Log-Likelihood</i>	-738.0	-741.9	-736.5

**(b) With carrying capacity**

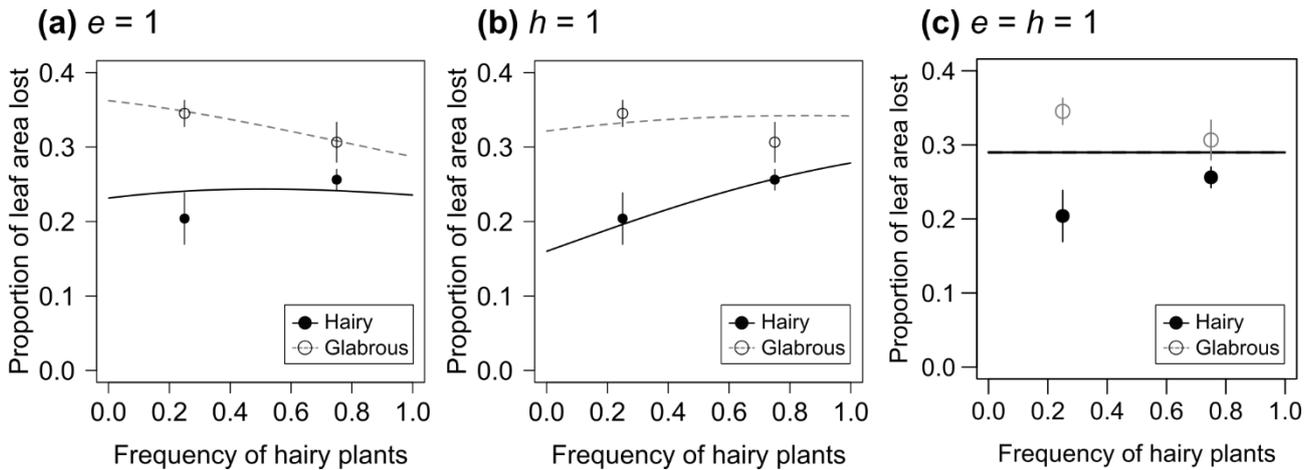
Parameter	Description	Percentiles		
		Median	2.5%	97.5%
$R'$	Transformed growth rate	1.79	1.38	2.32
$c'$	Transformed cost of defence	-0.03	-0.40	0.34
$k$	Inverse of carrying capacity ( $0 < k < 1$ )	$<10^{-21}$	$<10^{-67}$	$<10^{-3}$
$d$	Proportion of interpatch dispersal	0.11	0.08	0.14
$m$	Mortality	0.75	0.69	0.80
---	<i>Log-Likelihood</i>	-738.0	-741.7	-736.6

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916 **Figure S1** Prediction of leaf damage (evaluated by the proportion of leaf area lost to

917 herbivory; mean  $\pm$  SE) in hairy (solid line with closed circles) and glabrous (dashed line with

918 open circles) plants in a laboratory by using ODC model. Panels (a), (b), and (c) present the

919 results when no differences were assumed between hairy and glabrous plants in energy intake

920 (i.e.  $e = 1$ ), handling time ( $h = 1$ ), and both ( $e = h = 1$ ), respectively. However, the estimated

921 leaf damage of hairy and glabrous plants (solid and dashed lines) cannot explain the leaf

922 damage observed in empirical data (open and closed circle, respectively). Parameter values

923 are at  $h = 2.10$ ,  $s = 1.76$ ,  $\alpha = 0.95$  in the case  $e = 1$ ;  $e = 0.32$ ,  $s = 2.11$ ,  $\alpha = 1.49$  in the case  $h =$

924 1; and  $s = 2.456$ ,  $\alpha = 0.685$  in the case  $e = h = 1$ .

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934 **Appendix S6. The condition for the coexistence of hairy and glabrous plants**

935 First, we calculate the frequency of hairy plants at a stable state. The relative amounts of  
 936 offspring per one glabrous and one hairy plant are obtained by dividing Eq. (7a) and (7b) by  
 937  $Rn_g$  and  $Rn_h$ , respectively, i.e.

938 
$$1 - \frac{v}{s + (1 - f) + fhD(f)} \quad \text{and} \quad \text{Eq. (S9a)}$$

939 
$$1 - \frac{D(f)}{s + (1 - f) + fhD(f)} - c. \quad \text{Eq. (S9b)}$$

940 Because herbivory has negligible effects on mortality ( $m_d$ ; see Table 1 in the main text),  
 941 glabrous and hairy plants differ only in the damage and the cost of defence in this model. The  
 942 fitness of glabrous and hairy plants are, therefore, proportional to Eq. (S9a) and (S9b),  
 943 respectively. By solving the condition that Eq. (S9a) is equal to Eq. (S9b), we can investigate  
 944 the frequency of hairy plants at a stable state, i.e.

945 
$$\frac{v}{s + (1 - f^*) + f^*hD(f^*)} = \frac{vD(f^*)}{s + (1 - f^*) + fhD(f^*)} + c. \quad \text{Eq. (S10)}$$

946 By solving Eq. (S10), we obtained the equilibrium frequency of hairy plants  $f^*$  at the stable  
 947 state.

948 Next, we investigated the condition for the coexistence of hairy and glabrous plants.

949 Let us consider the situation that population is filled by glabrous plants, i.e.  $f = 0$ . For the  
 950 invasion of the population by hairy plants, the number of offspring of hairy plants per capita  
 951 should be larger than that of glabrous plants, i.e.

952 
$$1 - \frac{v}{s + 1} > 1 - \frac{vD(0)}{s + 1} - c. \quad \text{Eq. (S11)}$$

953 By solving this, we obtain

954 
$$1 < \frac{1}{1 + \exp[\alpha f^*]} + \frac{c(s + 1)}{v}. \quad \text{Eq. (S12)}$$

955 If Eq. (S12) is satisfied, a hairy plant can potentially invade the population of glabrous plants.  
956 Similarly, for the invasion of the population of hairy plants by glabrous plants, the number of  
957 offspring of glabrous plants per capita should be larger than that of hairy plants, i.e.

$$958 \quad 1 - \frac{v}{s + hD(1)} > 1 - \frac{vD(1)}{s + hD(1)} - c. \quad \text{Eq. (S13)}$$

959 By solving this, we obtain

$$960 \quad 1 < \frac{1}{1 + \exp[-\alpha(1 - f^*)]} \left( 1 + \frac{c}{v} \right) + \frac{cs}{v}. \quad \text{Eq. (S14)}$$

961 If Eq. (S14) is satisfied, a glabrous plant can potentially invade the population of hairy plants.  
962 Consequently, two morphs can coexist if both Eq. (S12) and Eq. (S14) are simultaneously  
963 satisfied.  
964