

1 **The evolvability of animal-pollinated flowers: towards predicting**
2 **adaptation to novel pollinator communities**

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10 Running head: The evolvability of flowers

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12 Summary, 187 words; Main text, 3858 words (Introduction, 1128 words; Materials and
13 Methods, 472 words; Results, 304 words; Discussion, 1893 words, Acknowledgements, 61
14 words). Three figures (Figs. 1 and 2 in colour), 1 table, 2 supporting files

15 **Summary**

16 1. In the event of a community turnover, population decline, or complete disappearance of
17 pollinators, animal-pollinated plants may respond by adapting to novel pollinators or by
18 changing their mating system. The ability of populations to adapt is determined by their
19 ability to respond to novel selection pressures, i.e. their evolvability. On the short term,
20 evolvability is determined by standing genetic variation in the trait under selection.

21 2. To evaluate the evolutionary potential of plant reproductive systems, I compiled genetic-
22 variance estimates for a large selection of floral traits mediating shifts in pollination and
23 mating systems. Then, I computed evolvabilities and compared these among trait groups and
24 against the evolvabilities of vegetative traits.

25 3. Evolvabilities of most floral traits were substantial yet tended to be lower than the median
26 for vegetative traits. Among floral traits, herkogamy (anther-stigma distance), floral-display
27 traits and perhaps floral-volatile concentrations had greater-than-average evolvabilities, while
28 the evolvabilities of pollinator-fit traits were below average.

29 4. These results suggest that most floral traits have the potential to evolve rapidly in response
30 to novel selection pressures, providing resilience of plant reproductive systems in the event of
31 changing pollinator communities.

32

33 Key words: Berg hypothesis, evolvability, floral trait, heritability, plant-pollinator
34 interactions, pollinator decline

35 **Introduction**

36 The ecology and evolution of flowers stands at the very centre of plant reproductive biology
37 (Lloyd & Barrett, 1996; Harder & Barrett, 2006; Harder & Johnson, 2009). The importance of
38 pollination biology and pollinator-mediated selection on floral traits for the diversification of
39 plant lineages has long been recognized (e.g. Darwin, 1862; Stebbins, 1970), and constitutes a
40 major research program in evolutionary biology (van der Niet *et al.*, 2014). In the light of
41 ongoing changes in species assemblages worldwide, including recent declines in pollinator
42 populations (Potts *et al.*, 2010; Gonzalez-Varo *et al.*, 2013), our knowledge of floral evolution
43 is becoming exposed to the ultimate test: Can we, based on our current understanding, predict
44 the consequences of environmental perturbations such as the loss or decline of a pollinator
45 species?

46 It is useful to consider evolution by natural selection as a two-step process: selection
47 acting on phenotypic traits, and the ability of these traits to evolve (i.e. their evolvability). A
48 community turnover, population decline, or complete disappearance of pollinators will
49 impose novel selection pressures on flowers, and the evolutionary potential of plant
50 reproductive systems depends on the ability of plant populations to respond to this selection
51 (Mitchell & Ashman, 2008; Eckert *et al.*, 2010; Thomann *et al.*, 2013). The separation of
52 selection from evolvability is made mathematically explicit by Lande's (1979) selection-
53 response equation, $\Delta z = V_A \beta$, where Δz is the change in the trait mean in response to an
54 episode of selection, V_A is the additive genetic variance, and β is the selection gradient, the
55 regression slope of relative fitness on trait z . This simple equation provides a theoretical
56 framework for obtaining meaningful measures of the two central components of evolution;
57 natural selection (Lande & Arnold, 1983; Hereford *et al.*, 2004) and evolvability (Houle,
58 1992; Hansen *et al.*, 2011). These measures can then be used to compute important
59 parameters such as the expected response to an episode of selection, or the number of
60 generations needed to change the trait mean by a given percentage under a given strength of
61 selection.

62 Although an extensive literature exists on the evolutionary potential of floral traits
63 mediating plant-pollinator interactions and plant mating systems, generalization and synthesis
64 has been difficult. This is in part due to the common treatment of heritability, the proportion
65 of phenotypic variance due to genetic effects, as the currency of evolutionary potential. While
66 heritability is a useful metric for predicting response to selection, as illustrated by its wide use
67 in plant and animal breeding, its use as a standardized measure of evolutionary potential has
68 been criticized on several grounds (Houle, 1992; Hansen *et al.*, 2011). While the Lande

69 equation cleanly separates selection from evolvability, this separation is broken by variance-
70 standardization (Hereford *et al.* 2004). Furthermore, due to correlations between additive-
71 genetic and other components of the phenotypic variance, heritabilities are largely
72 uncorrelated with additive genetic variances (Hansen *et al.* 2011). Therefore, there is reason
73 to suspect that some of the conclusions drawn from previous syntheses of plant evolutionary
74 potentials (Geber & Griffen, 2003; Ashman & Majetic, 2006; Harder & Johnson, 2009) may
75 change when considering evolutionary potential on a different scale. In the following
76 synthesis of floral evolvabilities, I will use mean-scaled genetic variance as a standardized
77 measure of evolvability (Houle, 1992; Hansen & Houle, 2008; Hansen *et al.*, 2011). This
78 measure has a straightforward interpretation as the expected evolutionary response, in
79 percentage of the trait mean, to an episode of unit strength selection. Conveniently, unit
80 strength selection is the strength of selection on fitness as a trait, providing a useful
81 benchmark (Hereford *et al.* 2004).

82 The choice of measurement scale and standardisation is an important step in any
83 analysis, and can strongly influence the conclusions of comparative studies. A classic
84 example is the contrasting conclusions drawn about the evolutionary potentials of life-history
85 vs. morphological traits: while life-history traits tend to be less heritable than are
86 morphological traits (Mousseau & Roff, 1987), the opposite is true for mean-scaled
87 evolvabilities (Houle, 1992). This effect arises because life-history traits tend to exhibit both
88 greater genetic variances and greater total phenotypic variances than do morphological traits,
89 and heritabilities therefore act as a ‘rubber scale’ that stretches when we are measuring
90 something large (see Hansen *et al.* 2011 for further discussion of the measurement of
91 evolvability).

92 Variational properties and how these are shaped by historical selection are particularly
93 important for understanding the evolvability of floral traits. Because effective pollen transfer
94 depends on precise fit of flowers and pollinators, floral traits in animal-pollinated species are
95 expected to be less sensitive to environmental variation, and thus less variable, than are
96 vegetative traits (Berg, 1960; Armbruster *et al.*, 1999; Pélabon *et al.*, 2011). However, it is not
97 well understood whether and how the different environmental sensitivities of floral and
98 vegetative traits affect their evolvabilities, and the relationship between genetic and
99 environmental (non-genetic) variances (Conner & Via, 1993; Hansen *et al.*, 2007). An
100 interesting possibility is that pollinator-mediated stabilizing selection on floral dimensions
101 could lead both to environmental canalization and loss of standing genetic variation, thus
102 resulting in reduced evolvability of those traits important for adaptation to novel pollinator

103 communities. Alternatively, a history of variable pollinator communities would suggest
104 fluctuating selection and perhaps maintenance of standing genetic variation in pollination
105 traits (Bell, 2010).

106 Different kinds of reproductive shifts are likely to involve changes in different sets of
107 floral traits. For example, shifts in principal pollinator species will often involve evolution of
108 traits mediating either pollinator attraction (reward or advertisement), flower-pollinator fit, or
109 both (e.g. Armbruster, 1988; Galen, 1996; Campbell *et al.*, 1997; Bradshaw & Schemske,
110 2003; Kay & Schemske, 2003; Kaczorowski *et al.*, 2005; Whittall & Hodges, 2007; Anderson
111 & Johnson, 2008; Smith *et al.*, 2008). Pollinator attraction can in turn be mediated by visual
112 (e.g. corolla size) or chemical (e.g. fragrance chemical composition) signals, and flower-
113 pollinator fit can depend among other things on the positions of sexual organs and the
114 dimensions of floral tubes. Finally, reduced reliability of pollination is often associated with
115 shifts in mating systems (rate of self-pollination), and will typically involve changes in traits
116 conferring reproductive assurance, notably herkogamy and dichogamy (e.g. Moeller, 2006;
117 Dart *et al.*, 2012; Opedal *et al.*, 2016; Briscoe Runquist *et al.*, 2017; Opedal *et al.*, 2017).
118 Therefore, a predictive understanding of plant adaptation to novel pollinator communities will
119 also require knowledge of variation in evolvabilities among trait groups.

120 Here, I aim to synthesize our current knowledge of floral evolvability. Using a large
121 database of plant evolvabilities compiled from the literature, I first assess the distribution of
122 evolvabilities among floral traits and discuss how and why floral evolvabilities differ from the
123 evolvabilities of vegetative traits. Then, I compare evolvabilities among groups of floral traits
124 mediating different kinds of reproductive shifts, focusing on those traits mediating pollinator
125 attraction, flower-pollinator fit, and plant mating systems.

126

127 **Materials and Methods**

128 *Literature survey*

129 To explore patterns of floral evolvability, I expanded the database analysed in Opedal *et al.*
130 (2017), broadly following the methods and criteria outlined therein. I extended the number of
131 floral trait categories (Supporting Information, Table S1), and included a sample of vegetative
132 traits (Table S2) for comparison. My focus is on animal-pollinated flowers, yet I also included
133 a few non-graminoid wind-pollinated species. Because I was interested in broad patterns of
134 genetic and non-genetic (residual) variance components across trait categories, I included
135 broad-sense as well as additive genetic variances.

136 To assess variation in evolvabilities among trait groups, I grouped the floral traits
137 according to their function in plant-pollinator interactions (Table S1): (1) Flower-pollinator fit
138 traits were those assumed to directly effect the accuracy of pollen transfer to and from the
139 bodies of pollinators, including sizes and positions of male and female sexual organs, and the
140 widths and lengths of floral tubes. (2) Flower size traits included any measure of the size of
141 individual flowers, most commonly corolla diameter and petal length. (3) Floral display traits
142 included any measure of the total size of floral displays, often flower or inflorescence number.
143 (4) Reward traits were those representing the amount of reward produced or the rate of reward
144 secretion. (5) Herkogamy was measured on a ratio scale as defined in Opedal *et al.* (2017), i.e.
145 as absolute anther-stigma distance.

146 Many studies reported only heritabilities, and not genetic variances or evolvabilities.
147 Whenever possible, I backcalculated genetic variances as $V_G = h^2 V_P$. Then, I computed
148 evolvabilities as $e = V_G/x^2$, where x is the trait mean. To compare the overall proportional
149 variance of each trait, I also computed mean-scaled residual variances as $I_R = e(1-h^2)/h^2$. For
150 heritabilities of zero, I used $I_R = V_P/x^2$, and for traits on a natural log scale I used $I_R = V_P - V_A$.
151 Mean-scaled residual variances are on the same proportional (%) scale as evolvabilities, and
152 are therefore informative about variational properties and can be compared among trait
153 groups. Studies failing to report trait means or other necessary summary statistics were
154 excluded. In a few cases, I contacted authors to obtain the necessary data.

155 *Analyses*

156 Due to the heterogeneous nature of the data, and incomplete reporting of standard errors, I
157 chose not to perform a formal meta-analysis (Morrissey, 2016). In the following, I report
158 median evolvabilities with 95% confidence intervals obtained from 10000 non-parametric
159 bootstrap estimates at the level of individual estimates. I report medians across all estimates,
160 and note where analyses restricted to additive genetic variances only yield qualitatively
161 different results. To estimate the variance in evolvabilities explained by trait group and by
162 sub-groups within trait groups, I fitted linear mixed-effects models to log-transformed
163 evolvability data where trait group and sub-group nested within trait group were random
164 factors. Analyses were performed in R 3.5.0 (R Core Team, 2018).

165

166 **Results**

167 *Database description*

168 The updated database (Table S3) contains 792 evolvability estimates for 54 taxa representing
169 27 families. Among the 72 studies included, 68.6% were conducted on populations
170 originating in North America (Fig. S1). Most studies were conducted in glasshouses or other
171 controlled environments.

172 *Genetic and non-genetic variance components of floral and vegetative traits*

173 Evolvabilities varied widely within floral and vegetative traits (Fig. 1), and these broad
174 categories explained only 13.8% of the variance in evolvabilities. In the complete dataset, the
175 median evolvability of vegetative traits ($e = 2.08\%$, Table 1) was about twice as large as the
176 median for floral traits ($e = 0.98\%$). Similarly, the median mean-scaled residual variance was
177 greater for vegetative traits ($I_R = 7.21\%$, Table 1) than for floral traits ($I_R = 1.69\%$).
178 Evolvabilities and residual variances were positively correlated across trait groups ($r = 0.64$).
179 Notice that the proportional difference in residual variances between floral and vegetative
180 traits was greater than the proportional difference in evolvabilities (Fig. 1), corresponding to a
181 greater median heritability of floral traits ($h^2 = 0.35$, 95% CI = 0.32 - 0.38) than of vegetative
182 traits ($h^2 = 0.21$, 95% CI = 0.18 - 0.27). All patterns remained similar when the analysis was
183 restricted to additive genetic variances only, yet the narrow-sense (additive-genetic)
184 evolvabilities of floral and vegetative traits were more similar ($e = 0.92\%$ vs. 1.26% ,
185 respectively; Table 1).

186 *Comparison of evolvabilities among floral trait groups*

187 Evolvabilities varied widely within each of the floral-trait functional groups, with 22.7% of
188 the variance in evolvabilities explained by trait group, and 26.6% by subgroups within these
189 (Fig. 2). Evolvabilities of fit traits (median $e = 0.43\%$, Table 1), reward traits ($e = 0.45\%$) and
190 flower-size traits ($e = 0.64\%$) tended to be lower than the medians for display traits ($e =$
191 3.73%) and herkogamy ($e = 9.07\%$).

192 **Discussion**

193 Plant evolutionary response to changes in pollinator communities depends on the evolutionary
194 potential of floral traits mediating pollinator shifts and evolution of mating systems. In the
195 following, I outline general patterns emerging from published data on floral evolvability,
196 point to gaps in our current understanding of floral evolvability, and propose ways forward to
197 fill these gaps.

198 *The evolvability of floral and vegetative traits*

199 As predicted from the Berg hypothesis (Berg 1960, Armbruster *et al.* 1999, Pélabon *et al.*
200 2011), median residual variances in vegetative traits were fourfold greater than the median for
201 floral traits (Table 1). Although the simple measure of residual (non-genetic) variance used
202 here includes non-additive genetic variance components, and more studies explicitly
203 considering environmental variance components would be desirable (e.g. Ørsted *et al.*, 2017),
204 this result is consistent with the expectation of reduced environmental sensitivity of floral
205 traits compared to vegetative traits, assumingly as a result of pollinator-mediated canalizing
206 selection.

207 As pointed out by Houle (1992) and Hansen *et al.* (2011), additive, non-additive and
208 non-genetic components of the phenotypic variance tends to be positively correlated. The data
209 supported this, as evolvabilities tended also to be greater for vegetative traits than for floral
210 traits. The proportional difference was less than for the residual variances, however, resulting
211 in greater heritabilities of floral traits than of vegetative traits. This finding mirrors the
212 contrasting conclusions drawn about evolutionary potentials of morphological and life-history
213 traits, and illustrates the important consequences of the choice of measurement-scale and
214 standardization in comparative studies (Hansen *et al.*, 2011; Houle *et al.*, 2011). When the
215 analysis was restricted to additive variances only, median evolvabilities were detectably
216 reduced for vegetative traits, but not for floral traits. At face value this suggests a greater
217 influence of non-additive genetic effects on vegetative traits than on floral traits, although this
218 finding should be interpreted with care due to the smaller sample size for the vegetative traits.

219 The Berg hypothesis predicts reduced phenotypic variance of floral traits to ensure
220 effective pollen transfer. Thus, it also follows that those traits directly involved in the
221 mechanics of pollen transfer (or plant-pollinator fit) should perhaps exhibit reduced
222 phenotypic variances compared to floral traits not directly involved in pollen transfer. As
223 expected, pollinator-fit traits had both the lowest median evolvabilities and the lowest residual
224 variances (Table 1, Fig. S2). Flower size traits followed a similar pattern, while floral-display
225 and reward traits appeared less canalized. Taken together, these results suggest that pollinator-
226 mediated stabilizing selection on floral traits have shaped their variational properties, and
227 more so for those traits closely linked to the mechanics of pollen transfer. Nevertheless, the
228 evolvabilities of most fit traits were substantial, and greater than the median for
229 morphological traits in general (Hansen *et al.* 2011).

230

231 *Patterns of floral evolvabilities*

232 Although most floral traits were on average less evolvable than were vegetative traits, the
233 evolutionary half-time (the number of generations needed to half or double the trait value
234 under unit strength selection) for an average floral trait in the database would be only $t \approx$
235 $\ln(0.5)/0.0092 = 75$ generations. Thus, a main conclusion of the literature survey is that plant
236 reproductive systems can often respond rapidly to selection imposed by novel pollinator
237 communities, and that floral-trait evolution is unlikely to be strongly constrained by a lack of
238 evolvability. A second conclusion is that, because most of the variance in evolvabilities
239 occurred within rather than among trait groups, the evolutionary potentials of different kinds
240 of reproductive shifts are likely to be species-specific and might therefore be challenging to
241 predict.

242 Several patterns emerged from the comparison of evolvabilities among floral trait
243 categories. First, mating-system shifts mediated by changes in herkogamy (anther-stigma
244 distance) stands out as one of the most rapid possible responses to shifting pollination
245 environments (Fig. 2). As discussed in detail in Opedal *et al.* (2017), rapid proportional
246 changes in herkogamy are possible because the genetic variance in herkogamy is often of
247 comparable magnitude to that of the component traits (pistil and stamen lengths), while
248 average herkogamy is usually much less than average sexual organ lengths. High evolvability
249 combined with the strong selection on herkogamy expected in the event of reduced pollination
250 reliability (Mitchell & Ashman 2008) suggests that detectable evolutionary change in
251 herkogamy can be expected over only a few generations (Opedal *et al.* 2017).

252 Second, the size of floral displays appears more evolvable than the size of individual
253 flowers. This finding should be interpreted with some care, however, because this comparison
254 is confounded with trait measurement dimension, and evolvabilities are known to vary with
255 trait dimensionality (Houle, 1992; Hansen *et al.*, 2011). While 75% of display traits were
256 counts, 78% of flower-size traits were linear size measures, 8% were areas, and 10% were
257 volumes or masses. Assuming that dimensions are perfectly correlated, the evolvabilities of
258 traits measured as areas and volumes are expected to increase by a factor equal to the square
259 of the trait dimension (i.e. four and nine for areas and volumes, respectively). However, it is
260 not clear whether a similar scaling relationship applies to counts, and across a large sample of
261 plant and animal evolvabilities, traits on count scales were not dramatically more evolvable
262 than were those represented by linear size measures (Hansen *et al.*, 2011).

263 Third, the available data on reward traits suggests low median evolvabilities, high
264 residual variances, and consequently low heritabilities (e.g. Kaczorowski *et al.*, 2008). Shifts
265 in reward amounts appear important in pollinator shifts, and more data on the quantitative

266 genetics of nectar traits and other rewards are therefore needed (Mitchell, 2004). For example,
267 the commonly observed shift from bee to hummingbird pollination is often associated with
268 changes in the amount and/or concentration of nectar (Thomson & Wilson, 2008).

269 Finally, fit traits had the lowest median evolvabilities, suggesting that, at a given
270 strength of selection, rates of adaptation to pollinators of different size, tongue length, beak
271 length, or proboscis length might be slower than other kinds of reproductive shifts (but still
272 possibly rather fast, see e.g. Galen, 1996; Campbell *et al.*, 1997; Campbell *et al.*, 2018). This
273 finding was consistent across all kinds of fit traits considered, i.e. sizes and positions of male
274 and female sexual organs, and widths and lengths of floral tubes.

275 *Evolvability and the rate of adaptation*

276 The value of trait evolvabilities as predictive tools depends on their ability to predict the rate
277 of evolutionary divergence of populations and species. In other words, can macroevolutionary
278 patterns be predicted from microevolutionary studies within single populations (Hansen *et al.*,
279 2003; Hansen & Voje, 2011; Bolstad *et al.*, 2014; Houle *et al.*, 2017)? Empirical studies are
280 beginning to yield clues about the rate of adaptation to altered pollination environments.
281 Gervasi and Schiestl (2017) subjected *Brassica rapa* populations to either bumblebee or
282 hoverfly pollinators over 9 generations, and detected significant evolutionary change in
283 multiple traits: bumblebee-pollinated populations evolved higher concentrations of fragrant
284 volatiles involved in pollinator attraction, and hoverfly-pollinated populations evolved greater
285 rates of autonomous selfing. A rapid increase in the ability to self autonomously also occurred
286 in response to experimental pollinator exclusion from *Mimulus guttatus* flowers (Bodbyl
287 Roels & Kelly, 2011). By experimentally manipulating pollinator communities, these studies
288 have shown that when pollinator communities change abruptly, and selection is strong,
289 adaptation can occur rapidly.

290 Interestingly, both studies detected rapid evolution of traits exhibiting greater-than-
291 average evolvabilities. The increased rate of selfing in *M. guttatus* was associated with
292 reduced herkogamy (anther-stigma separation), which appears to be a highly evolvable trait
293 (Opedal *et al.*, 2017, and see Results). Similarly, the evolvability of volatile concentrations in
294 *Brassica rapa*, computed from the heritabilities reported by Zu *et al.* (2016), was very high
295 with a median of 32.3% (Table S3). Combining the evolvabilities of each volatile
296 concentration with the selection responses reported by Gervasi and Schiestl (2017) illustrates
297 the utility of mean-scaled evolvabilities in predicting evolutionary divergence (Bolstad *et al.*,
298 2014). I computed the proportional evolutionary divergence as the difference between the

299 mean phenotypes obtained in the bumblebee and hoverfly treatments, divided by the mean of
300 the control treatment. On this proportional scale, more evolvable traits had diverged more
301 between the pollinator treatments, and evolvabilities explained 63.8% of the variance in
302 evolutionary divergence (Fig. 3).

303 Studies of contemporary evolution in plant populations under natural selection regimes
304 are rare. A notable exception is the recent study of Campbell *et al.* (2018), who combined
305 heritability estimates from one population (Campbell, 1996) with multi-year phenotypic-
306 selection estimates (Campbell & Powers, 2015) and trait measurements to demonstrate
307 substantial evolutionary change in corolla length of *Ipomopsis aggregata* over only 5
308 generations of hummingbird-mediated selection. Mean corolla length increased by 2.43 mm,
309 or 8.72% of the trait mean (27.88 mm, data from Campbell & Powers 2015). An important
310 lesson from this study is that even traits with comparatively low evolvability can evolve
311 rapidly when selection is strong: the mean selection differential of 0.72 mm reported by
312 Campbell *et al.* (2018) translates into a mean-scaled selection gradient of 175%, i.e. nearly
313 twice as strong as selection on fitness as a trait (Hereford *et al.*, 2004). Thus, while a history
314 of strong selection on pollinator-fit traits may have reduced their genetic and phenotypic
315 variabilities, the same strong selection may allow renewed adaptation in the event of a sudden
316 shift in pollinator species.

317

318 *Perspectives*

319 While the evolvability of floral-morphology traits is increasingly well understood, the
320 evolvability of chemical signals remains an area in need of study. If the high evolvability of
321 fragrance phenotypes of the model species *Brassica rapa* is comparable to other systems, it
322 means that pollinator-attraction systems based on floral fragrance are highly evolvable. Such a
323 pattern would contribute to explain a striking biodiversity pattern, namely the astonishing
324 diversity of plants exhibiting floral-fragrance attraction systems, such as neotropical orchids
325 pollinated by male euglossine bees (e.g. *Gongora*, *Stanhopea*; Dodson *et al.*, 1969).

326 Pollinator shifts are often associated with divergence in colour, yet I failed to obtain
327 relevant data allowing me to evaluate the evolvability of colour. This might be partly due to
328 the difficulty in measuring colour on a ratio scale, but it should also be noted that evolutionary
329 shifts in colour seems at least in some cases to be controlled by major mutations, as in the
330 case of the well-studied shift to hummingbird pollination in *Mimulus cardinalis* (Bradshaw &
331 Schemske, 2003). Indeed, while I have focused here on the potential for adaptation from
332 standing genetic variation, other modes of evolution cannot be ignored.

333 Finally, single-trait evolvabilities are useful for predicting evolutionary response to
334 selection, yet traits involved in plant-pollinator interactions rarely evolve independently
335 (Stebbins, 1974). For example, flower size and shape often covary, so that adaptation to a
336 larger pollinator will often involve increases in both flower size and fit traits, and vice versa.
337 The same might be true for flower size and number, as the product of these two traits were
338 found to covary more closely with species' mating systems than did either trait alone
339 (Goodwillie *et al.*, 2010). Floral volatiles often act synergistically to attract pollinators, and if
340 pollinator shifts in these systems depend on specific interactions between volatiles, single-trait
341 evolvabilities might not be very useful. These considerations lead me to suggest that further
342 progress in understanding the evolvability of plant reproductive systems will require studies
343 of the evolvabilities of trait combinations, as represented by specific directions in multivariate
344 trait space. Methods are now available for addressing these questions (Hansen & Houle, 2008;
345 Bolstad *et al.*, 2014; Opedal *et al.*, 2017).

346

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485

Table 1. Median evolvabilities (e) and mean-scaled residual variances (I_R) per trait group, given as percentages (i.e. $\times 100$). Sample size (n) is the number of estimates per trait group.

Trait group	Evolvability (all data)		Evolvability (additive variances only)		Residual variance (all data)	
	n	e (95% CI)	n	e (95% CI)	n	I_R (95% CI)
Vegetative	152	2.08 (1.67, 2.45)	96	1.26 (0.96, 1.74)	150	7.21 (5.71, 11.20)
Floral (all)	528	0.98 (0.81, 1.16)	381	0.92 (0.72, 1.14)	488	1.69 (1.45, 2.06)
Floral display	73	3.73 (2.65, 6.31)	65	3.70 (1.94, 5.79)	68	11.75 (8.55, 15.38)
Flower size	127	0.64 (0.51, 0.80)	89	0.60 (0.45, 0.84)	124	0.96 (0.80, 1.44)
Reward	12	0.45 (0.16, 1.75)	12	0.45 (0.16, 1.75)	11	3.41 (1.21, 6.61)
Pollinator fit	96	0.43 (0.32, 0.49)	67	0.44 (0.38, 0.52)	91	0.53 (0.41, 0.72)
Herkogamy	34	9.07 (6.76, 13.09)	24	9.07 (5.82, 14.08)	10	11.21 (7.11, 18.86)

486

487 **Figure legends**

488 Fig. 1. Evolvabilities and mean-scaled residual phenotypic variances of vegetative (green
489 boxes) and floral (blue boxes) traits, given as percentages (i.e. multiplied by 100). Thick lines
490 across boxes indicate the median of each trait category, and thick lines within boxes indicate
491 median values for each trait sub-category. Boxes extend from the first to third quartile.
492 Sample sizes are given in parentheses for each trait sub-category. See Tables S1 and S2 for
493 details about trait categories.

494 Fig. 2. Evolvabilities of herkogamy, floral display traits, flower size traits, reward traits, and
495 flower-pollinator fit traits, given as percentages (i.e. multiplied by 100). Thick lines across
496 boxes indicate the median of each trait category, and thick lines within boxes indicate median
497 values for each trait sub-category. Boxes extend from the first to third quartile. Sample sizes
498 are given in parentheses for each trait sub-category.

499 Fig. 3. Relationship between evolvability and evolutionary divergence (proportional response
500 to experimental evolution) for 12 floral volatiles in *Brassica rapa* populations. Evolvabilities
501 were computed from the heritabilities reported in Zu *et al.* (2016), and proportional response
502 to experimental evolution was computed from data reported in Gervasi and Schiestl (2017).
503 Evolvabilities (on log scale) explain 63.8% of the variance. See text for details.

504

505 **Supporting Information**

506 Fig. S1. Map of study populations included in the evolvability database

507 Fig. S2. Mean-scaled residual variances of floral traits

508 Table S1. List of floral trait categories in the evolvability database, with examples of traits

509 Table S2. List of vegetative trait categories in the evolvability database, with examples of
510 traits

511 Table S3. Evolvability database