New Phytologist

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

Øystein H. Opedal[1,2]

[1]Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, NTNU, Trondheim 7491, Norway; [2]Research Centre for Ecological Change, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

Author for correspondence:
Øystein H. Opedal
Tel: +47 92233189
Email: oystein.opedal@helsinki.fi

Received: *29 May 2018*
Accepted: *23 July 2018*

New Phytologist (2018)
doi: 10.1111/nph.15403

Key words: Berg hypothesis, evolvability, floral trait, heritability, plant–pollinator interactions, pollinator decline.

Summary

- In the event of a community turnover, population decline, or complete disappearance of pollinators, animal-pollinated plants may respond by adapting to novel pollinators or by changing their mating system. The ability of populations to adapt is determined by their ability to respond to novel selection pressures, i.e. their evolvability. In the short term, evolvability is determined by standing genetic variation in the trait under selection.
- To evaluate the evolutionary potential of plant reproductive systems, I compiled genetic-variance estimates for a large selection of floral traits mediating shifts in pollination and mating systems. Then, I computed evolvabilities and compared these among trait groups and against the evolvabilities of vegetative traits.
- Evolvabilities of most floral traits were substantial yet tended to be lower than the median for vegetative traits. Among floral traits, herkogamy (anther–stigma distance), floral-display traits and perhaps floral-volatile concentrations had greater-than-average evolvabilities, while the evolvabilities of pollinator-fit traits were below average.
- These results suggest that most floral traits have the potential to evolve rapidly in response to novel selection pressures, providing resilience of plant reproductive systems in the event of changing pollinator communities.

Introduction

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

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

Although an extensive literature exists on the evolutionary potential of floral traits mediating plant–pollinator interactions and plant-mating systems, generalization and synthesis has been difficult. This fact is in part due to the common treatment of heritability, the proportion of phenotypic variance due to genetic effects, as the currency of evolutionary potential. While heritability is a useful metric for predicting response to selection, as illustrated by its wide use in plant and animal breeding, its use as a standardized measure of evolutionary potential has been criticized on several grounds (Houle, 1992; Hansen *et al.*, 2011). While the Lande equation cleanly separates selection from evolvability, this separation is blurred by variance standardization (Hereford *et al.*, 2004). Furthermore, due to correlations between additive genetic and other components of the phenotypic variance, heritabilities are largely uncorrelated with additive genetic variances (Hansen *et al.*, 2011). Therefore, there is reason to suspect that some of the conclusions drawn from previous syntheses of plant evolutionary potentials (Geber & Griffen, 2003; Ashman & Majetic, 2006; Harder & Johnson, 2009) may change when considering evolutionary potential on a different scale. In the following synthesis of floral evolvabilities, I will use mean-scaled genetic variance as a standardized measure of evolvability (Houle, 1992; Hansen & Houle, 2008; Hansen *et al.*, 2011). This measure has a straightforward interpretation as the expected evolutionary response, in percentage of the trait mean, to an episode of unit strength selection. Conveniently, unit strength selection is the strength of selection on fitness as a trait, providing a useful benchmark (Hereford *et al.*, 2004).

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

Variational properties and how these are shaped by historical selection are particularly important for understanding the evolvability of floral traits. Because effective pollen transfer depends on precise fit of flowers and pollinators, floral traits in animal-pollinated species are expected to be less sensitive to environmental variation and therefore less variable than vegetative traits (Berg, 1960; Armbruster *et al.*, 1999; Pélabon *et al.*, 2011). However, it is not well understood whether and how the different environmental sensitivities of floral and vegetative traits affect their evolvabilities, and the relationship between genetic and environmental (nongenetic) variances (Conner & Via, 1993; Hansen *et al.*, 2007). An interesting possibility is that pollinator-mediated stabilizing selection on floral dimensions could lead both to environmental canalization and to loss of standing genetic variation, therefore resulting in reduced evolvability of traits that are important for adaptation to novel pollinator communities. Alternatively, a history of variable pollinator communities would suggest fluctuating selection and perhaps maintenance of standing genetic variation in pollination traits (Bell, 2010).

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

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

Materials and Methods

Literature survey

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

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

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

Analyses

Due to the heterogeneous nature of the data, and incomplete reporting of standard errors, I chose not to perform a formal meta-analysis (Morrissey, 2016). In the following, I report median evolvabilities with 95% confidence intervals obtained from 10 000 nonparametric bootstrap estimates at the level of individual estimates. I report medians across all estimates, and note where analyses restricted to additive genetic variances only yield qualitatively different results. To estimate the variance in evolvabilities explained by trait groups and by sub-groups within trait groups, I fitted linear mixed-effects models to $\log_e$-transformed evolvability data where trait group and sub-group nested within trait group were random factors. Analyses were performed in R 3.5.0 (R Core Team, 2018).

Results

Database description

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

Genetic and nongenetic variance components of floral and vegetative traits

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

Comparison of evolvabilities among floral trait groups

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

Discussion

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

The evolvability of floral and vegetative traits

As predicted from the Berg hypothesis (Berg, 1960; Armbruster *et al.*, 1999; Pélabon *et al.*, 2011), median residual variances of vegetative traits were four-fold greater than the median for floral traits (Table 1). Although the simple measure of residual (nongenetic) variance used here includes nonadditive genetic variance components, and more studies that explicitly consider environmental variance components would be desirable (e.g. Ørsted *et al.*, 2017), the results detailed here are consistent with the expectation of reduced environmental sensitivity of floral traits compared with vegetative traits, assumingly as a result of pollinator-mediated canalizing selection.

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

The Berg hypothesis predicts reduced phenotypic variance of floral traits to ensure effective pollen transfer. Therefore, it also follows that those traits directly involved in the mechanics of pollen transfer (or plant–pollinator fit) should perhaps exhibit

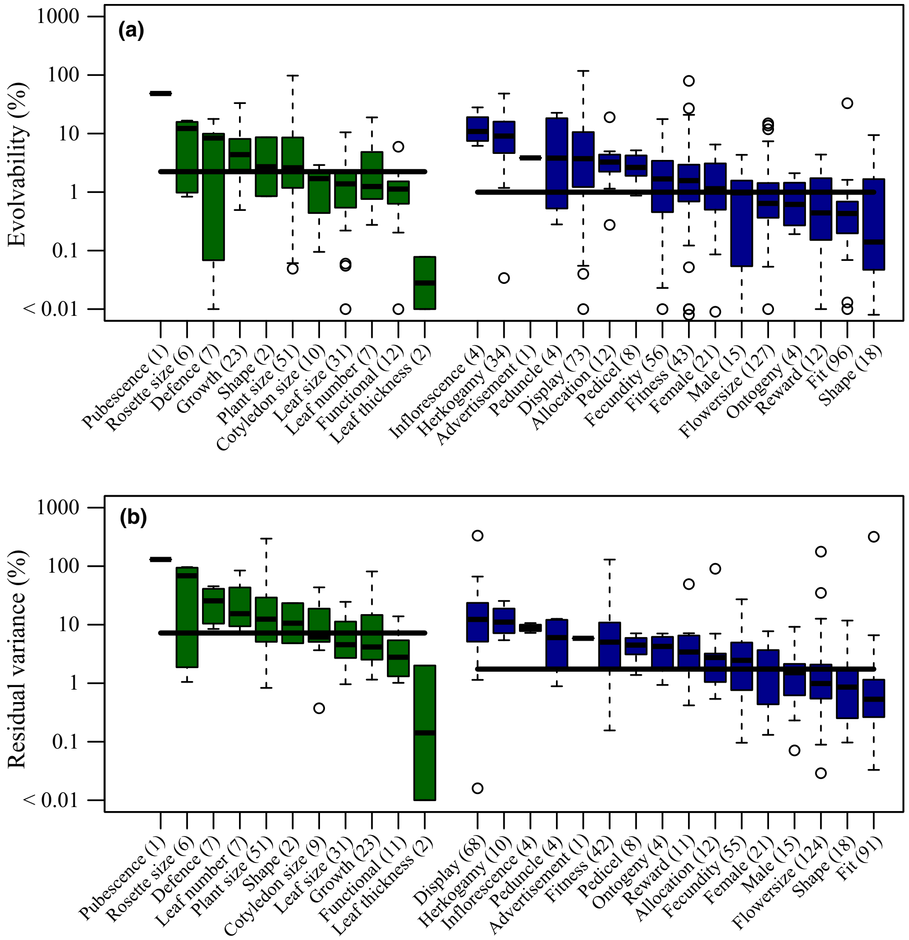

Fig. 1 (a) Evolvabilities and (b) mean-scaled residual phenotypic variances of vegetative (green boxes) and floral (blue boxes) traits, given as percentages (i.e. ×100). Thick lines across boxes indicate the median of each trait category, and thick lines within boxes indicate median values for each trait subcategory. Boxes extend from the first to third quartile, range bars extend to 1.5× the inter-quartile range, and data points outside this range are shown as open circles. Sample sizes are given in parentheses for each trait subcategory. See Supporting Information Tables S1 and S2 for details on trait categories.

Table 1 Median evolvabilities (*e*) and mean-scaled residual variances (I_R) per trait group, given as percentages (i.e. ×100)

	Evolvability (all data)		Evolvability (additive variances only)		Residual variance (all data)	
Trait group	*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)

Sample size (*n*) is the number of estimates per trait group.

reduced phenotypic variances compared with floral traits not directly involved in pollen transfer. As expected, pollinator-fit traits had both the lowest median evolvabilities and the lowest residual variances (Table 1; Fig. S2). Flower-size traits followed a similar pattern, while floral-display and reward traits appeared less canalized. Taken together, these results suggest that pollinator-mediated stabilizing selection on floral traits have shaped their variational properties, and more so for traits that are closely linked to the mechanics of pollen transfer. Nevertheless, the evolvabilities of most fit traits were substantial, and greater than the median for morphological traits in general (Hansen *et al.*, 2011).

Patterns of floral evolvabilities

Although most floral traits were on average less evolvable than were vegetative traits, the evolutionary halftime (the number of generations needed to half or double the trait value under unit strength selection) for an average floral trait in the database would be only $t_{½} \approx \log_e(0.5)/0.0092 = 75$ generations. Therefore, a

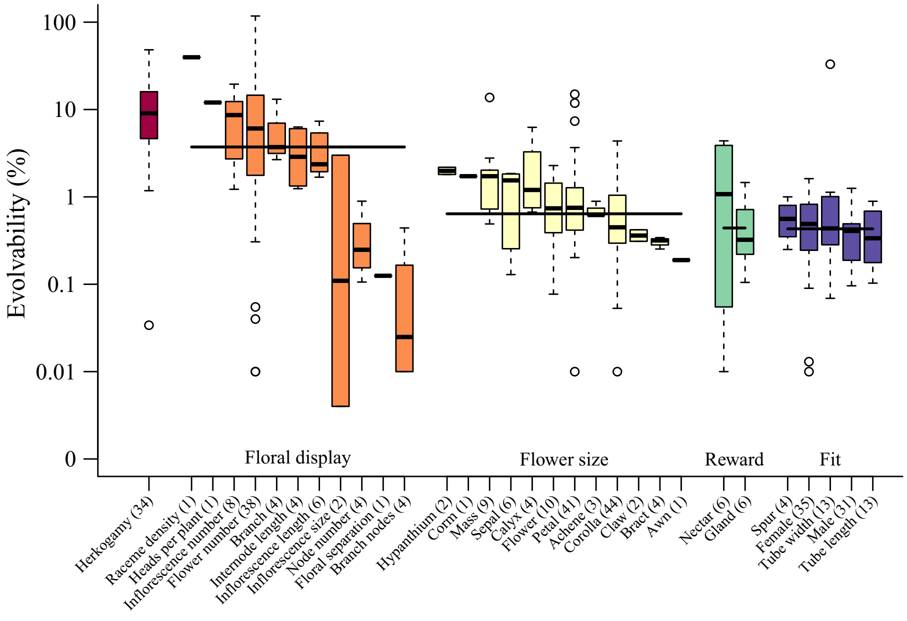

Fig. 2 Evolvabilities of herkogamy, floral-display traits, flower-size traits, reward traits, and flower-pollinator-fit traits, given as percentages (i.e. ×100). Thick lines across boxes indicate the median of each trait category, and thick lines within boxes indicate median values for each trait subcategory. Boxes extend from the first to third quartile, range bars extend to 1.5× the inter-quartile range, and data points outside this range are shown as open circles. Sample sizes are given in parentheses for each trait subcategory.

main conclusion of the literature survey is that plant reproductive systems can often respond rapidly to selection imposed by novel pollinator communities, and that floral-trait evolution is unlikely to be strongly constrained by a lack of evolvability. A second conclusion is that, because most of the variance in evolvabilities occurred within, rather than among, trait groups, the evolutionary potentials of different kinds of reproductive shifts are likely to be species specific and might therefore be challenging to predict.

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

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

Third, the available data on reward traits suggest low median evolvabilities, high residual variances and, consequently, low heritabilities (e.g. Kaczorowski *et al.*, 2008). Shifts in reward amounts appear important in pollinator shifts, and more data on the quantitative genetics of nectar traits and other rewards are therefore needed (Mitchell, 2004). For example, the commonly observed shift from bee to hummingbird pollination is often associated with changes in the amount and/or concentration of nectar (Thomson & Wilson, 2008).

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

Evolvability and the rate of adaptation

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

Interestingly, both studies detected rapid evolution of traits that exhibited greater-than-average evolvabilities. The increased rate of selfing in *M. guttatus* was associated with reduced herkogamy (anther–stigma separation), which appears to be a highly evolvable trait (Opedal *et al.*, 2017; and see Results). Similarly, the evolvability of volatile concentrations in *Brassica rapa*, computed from the heritabilities reported by Zu *et al.* (2016), was very high with a median of 32.3% (Table S3). Combining the evolvabilities of each volatile concentration with the selection responses reported by Gervasi & Schiestl (2017) illustrates the utility of mean-scaled evolvabilities in predicting evolutionary divergence (Bolstad *et al.*, 2014). I computed the proportional evolutionary divergence as the difference between the mean phenotypes obtained in the bumblebee and hoverfly treatments, divided by the mean of the control treatment. On this proportional scale, more evolvable traits had diverged more between the pollinator treatments, and evolvabilities explained 63.8% of the variance in evolutionary divergence (Fig. 3).

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

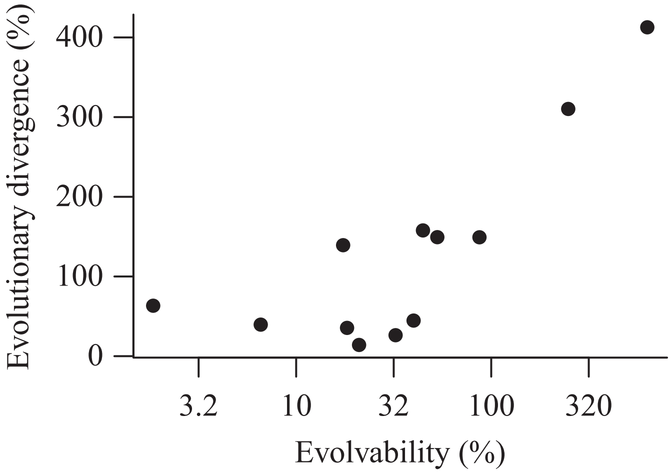

Fig. 3 Relationship between evolvability and evolutionary divergence (proportional response to experimental evolution) for 12 floral volatiles in *Brassica rapa* populations. Evolvabilities were computed from the heritabilities reported in Zu *et al.* (2016), and proportional response to experimental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

Perspectives

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

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

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

Acknowledgements

I thank S. Andersson and R. Smith for providing unpublished data, three anonymous reviewers for constructive comments on the manuscript, and C. Pélabon, W. S. Armbruster, G. H. Bolstad and T. F. Hansen for years of discussions related to the topic of this paper. This work was supported by the Research Council of Norway through its Centres of Excellence funding scheme, project no. 223257.

ORCID

Øystein H. Opedal http://orcid.org/0000-0002-7841-6933

References

Anderson B, Johnson SD. 2008. The geographical mosaic of coevolution in a plant-pollinator mutualism. *Evolution* **62**: 220–225.

Armbruster WS. 1988. Multilevel comparative analysis of the morphology, function, and evolution of *Dalechampia* blossoms. *Ecology* **69**: 1746–1761.

Armbruster WS, Di Stilio VS, Tuxill JD, Flores TC, Runk JLV. 1999. Covariance and decoupling of floral and vegetative traits in nine neotropical plants: a re-evaluation of Berg's correlation-pleiades concept. *American Journal of Botany* **86**: 39–55.

Ashman TL, Majetic CJ. 2006. Genetic constraints on floral evolution: a review and evaluation of patterns. *Heredity* **96**: 343–352.

Bell G. 2010. Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Philosophical Transactions of the Royal Society of London. Series B: Biological sciences* **365**: 87–97.

Berg RL. 1960. The ecological significance of correlation pleiades. *Evolution* **14**: 171–180.

Bodbyl Roels SA, Kelly JK. 2011. Rapid evolution caused by pollinator loss in *Mimulus guttatus*. *Evolution* **65**: 2541–2552.

Bolstad GH, Hansen TF, Pélabon C, Falahati-Anbaran M, Pérez-Barrales R, Armbruster WS. 2014. Genetic constraints predict evolutionary divergence in *Dalechampia* blossoms. *Philosophical Transactions of the Royal Society of London. Series B: Biological sciences* **369**: 20130255.

Bradshaw AD, Schemske DW. 2003. Allele substitution at a flower colour locus produces a pollinator shift in monkeyflowers. *Nature* **426**: 176–178.

Briscoe Runquist RD, Geber MA, Pickett-Leonard M, Moeller DA, Eckert CG, Winn AA. 2017. Mating system evolution under strong pollen limitation: evidence of disruptive selection through male and female fitness in *Clarkia xantiana*. *American Naturalist* **189**: 549–563.

Campbell DR. 1996. Evolution of floral traits in a hermaphroditic plant: field measurements of heritabilities and genetic correlations. *Evolution* **50**: 1442–1453.

Campbell DR, Faidiga A, Trujillo G. 2018. Clines in traits compared over two decades in a plant hybrid zone. *Annals of Botany* **122**: 315–324.

Campbell DR, Powers JM. 2015. Natural selection on floral morphology can be influenced by climate. *Proceedings of the Royal Society B: Biological Sciences* **282**: 20150178.

Campbell DR, Waser NM, Melendez-Ackerman EJ. 1997. Analyzing pollinator-mediated selection in a plant hybrid zone: hummingbird visitation patterns on three spatial scales. *American Naturalist* **149**: 295–315.

Conner J, Via S. 1993. Patterns of phenotypic and genetic correlations among morphological and life-history traits in wild radish, *Raphanus raphanistrum*. *Evolution* **47**: 704–711.

Dart SR, Samis KE, Austen E, Eckert CG. 2012. Broad geographic covariation between floral traits and the mating system in *Camissoniopsis cheiranthifolia* (Onagraceae): multiple stable mixed mating systems across the species range? *Annals of Botany* **109**: 599–611.

Darwin CR. 1862. *On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing*. London, UK: John Murray.

Dodson CH, Dressler RL, Hills HG, Adams RM, Williams NH. 1969. Biologically active compounds in orchid fragrances. *Science* **164**: 1243–1250.

Eckert CG, Kalisz S, Geber MA, Sargent R, Elle E, Cheptou PO, Goodwillie C, Johnston MO, Kelly JK, Moeller DA *et al.* 2010. Plant mating systems in a changing world. *Trends in Ecology and Evolution* **25**: 35–43.

Galen C. 1996. Rates of floral evolution: adaptation to bumblebee pollination in an alpine wildflower, *Polemonium viscosum*. *Evolution* **50**: 120–125.

Geber MA, Griffen LR. 2003. Inheritance and natural selection on functional traits. *International Journal of Plant Sciences* **164**: S21–S42.

Gervasi DD, Schiestl FP. 2017. Real-time divergent evolution in plants driven by pollinators. *Nature Communications* **8**: 14691.

Gonzalez-Varo JP, Biesmeijer JC, Bommarco R, Potts SG, Schweiger O, Smith HG, Steffan-Dewenter I, Szentgyoergyi H, Woyciechowski M, Vila M. 2013. Combined effects of global change pressures on animal-mediated pollination. *Trends in Ecology & Evolution* **28**: 524–530.

Goodwillie C, Sargent RD, Eckert CG, Elle E, Geber MA, Johnston MO, Kalisz S, Moeller DA, Ree RH, Vallejo-Marin M *et al.* 2010. Correlated evolution of mating system and floral display traits in flowering plants and its implications for the distribution of mating system variation. *New Phytologist* **185**: 311–321.

Hansen TF, Houle D. 2008. Measuring and comparing evolvability and constraint in multivariate characters. *Journal of Evolutionary Biology* **21**: 1201–1219.

Hansen TF, Pelabon C, Armbruster WS. 2007. Comparing variational properties of homologous floral and vegetative characters in *Dalechampia scandens*: testing the Berg hypothesis. *Evolutionary Biology* **34**: 86–98.

Hansen TF, Pélabon C, Armbruster WS, Carlson ML. 2003. Evolvability and genetic constraint in *Dalechampia* blossoms: components of variance and measures of evolvability. *Journal of Evolutionary Biology* **16**: 754–766.

Hansen TF, Pélabon C, Houle D. 2011. Heritability is not evolvability. *Evolutionary Biology* **38**: 258–277.

Hansen TF, Voje KL. 2011. Deviation from the line of least resistance does not exclude genetic constraints: a comment on Berner *et al.* (2010). *Evolution* **65**: 1821–1822.

Harder LD, Barrett SCH. 2006. *Ecology and evolution of flowers*. Oxford, UK: Oxford University Press.

Harder LD, Johnson SD. 2009. Darwin's beautiful contrivances: evolutionary and functional evidence for floral adaptation. *New Phytologist* **183**: 530–545.

Hereford J, Hansen TF, Houle D. 2004. Comparing strengths of directional selection: how strong is strong? *Evolution* **58**: 2133–2143.

Houle D. 1992. Comparing evolvability and variability of quantitative traits. *Genetics* **130**: 195–204.

Houle D, Bolstad GH, van der Linde K, Hansen TF. 2017. Mutation predicts 40 million years of fly wing evolution. *Nature* **548**: 447–450.

Houle D, Pélabon C, Wagner GP, Hansen TF. 2011. Measurement and meaning in biology. *Quarterly Review of Biology* **86**: 3–34.

Kaczorowski RL, Gardener MC, Holtsford TP. 2005. Nectar traits in *Nicotiana* section Alatae (Solanaceae) in relation to floral traits, pollinators, and mating system. *American Journal of Botany* **92**: 1270–1283.

Kaczorowski RL, Juenger TE, Holtsford TR. 2008. Heritability and correlation structure of nectar and floral morphology traits in *Nicotiana alata*. *Evolution* **62**: 1738–1750.

Kay KM, Schemske DW. 2003. Pollinator assemblages and visitation rates for 11 species of neotropical *Costus* (Costaceae). *Biotropica* **35**: 198.

Lande R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* **33**: 402–416.

Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. *Evolution* **37**: 1210–1226.

Lloyd DG, Barrett SC. 1996. *Floral biology: studies of floral evolution in animal-pollinated plants*. New York, NY, USA: Chapman & Hall.

Mitchell RJ. 2004. Heritability of nectar traits: why do we know so little? *Ecology* **85**: 1527–1533.

Mitchell RJ, Ashman T-L. 2008. Predicting evolutionary consequences of pollinator declines: the long and short of floral evolution. *New Phytologist* **177**: 576–579.

Moeller DA. 2006. Geographic structure of pollinator communities, reproductive assurance, and the evolution of self-pollination. *Ecology* **87**: 1510–1522.

Morrissey MB. 2016. Meta-analysis of magnitudes, differences and variation in evolutionary parameters. *Journal of Evolutionary Biology* **29**: 1882–1904.

Mousseau TA, Roff DA. 1987. Natural selection and the heritability of fitness components. *Heredity* **59**: 181–197.

van der Niet T, Peakall R, Johnson SD. 2014. Pollinator-driven ecological speciation in plants: new evidence and future perspectives. *Annals of Botany* **113**: 199–211.

Opedal ØH, Albertsen E, Armbruster WS, Pérez-Barrales R, Falahati-Anbaran M, Pélabon C. 2016. Evolutionary consequences of ecological factors: pollinator reliability predicts mating-system traits of a perennial plant. *Ecology Letters* **19**: 1486–1495.

Opedal ØH, Bolstad GH, Hansen TF, Armbruster WS, Pélabon C. 2017. The evolvability of herkogamy: quantifying the evolutionary potential of a composite trait. *Evolution* **71**: 1572–1586.

Ørsted M, Rohde PD, Hoffmann AA, Sorensen P, Kristensen TN. 2017. Environmental variation partitioned into separate heritable components. *Evolution* **72**: 136–152.

Pélabon C, Armbruster WS, Hansen TF. 2011. Experimental evidence for the Berg hypothesis: vegetative traits are more sensitive than pollination traits to environmental variation. *Functional Ecology* **25**: 247–257.

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* **25**: 345–353.

R Core Team. 2018. *R: a language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Smith SD, Ane C, Baum DA. 2008. The role of pollinator shifts in the floral diversification of *Iochroma* (Solanaceae). *Evolution* **62**: 793–806.

Stebbins GL. 1970. Adaptive radiation of reproductive characteristics in angiosperms, I: Pollination mechanisms. *Annual Review of Ecology and Systematics* **1**: 307–326.

Stebbins GL. 1974. *Flowering plants: evolution above the species level.* Cambridge, MA, USA: Belknap Press.

Thomann M, Imbert E, Devaux C, Cheptou P-O. 2013. Flowering plants under global pollinator decline. *Trends in Plant Science* **18**: 353–359.

Thomson James D, Wilson P. 2008. Explaining evolutionary shifts between bee and hummingbird pollination: convergence, divergence, and directionality. *International Journal of Plant Sciences* **169**: 23–38.

Whittall JB, Hodges SA. 2007. Pollinator shifts drive increasingly long nectar spurs in columbine flowers. *Nature* **447**: 706–709.

Zu P, Blanckenhorn WU, Schiestl FP. 2016. Heritability of floral volatiles and pleiotropic responses to artificial selection in *Brassica rapa*. *New Phytologist* **209**: 1208–1219.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article:

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

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

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

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

Table S3 Evolvability database