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APPENDIX 1. A SURVEY OF PHENOTYPIC SELECTION ON POLLINATION TRAITS

METHODS

STUDY SELECTION

The aim of this survey was to assess broad patterns of strength and variation in selection on pollination traits. To this end, I compiled a database of selection estimates with spatial or temporal replication. I selected studies based on a comprehensive review of the literature during the preparation of the present paper but did not perform systematic database searches. I consider the included studies to be representative of studies replicated over multiple populations or years. The included studies focused on plant-pollinator interactions or (at least) phenotypic selection on floral traits. I considered ‘pollination traits’ to include floral traits as well as other traits often perceived to be important for plant-pollinator interactions and thus assessed in studies focusing on pollinator-mediated selection, such as plant size (height) and flowering phenology.

I included both studies considering open-pollinated plants only (thus estimating net selection), and those explicitly aiming to disentangle pollinator-mediated selection through either supplemental pollination treatments, or statistically through a fitness function. For each study, I included those estimates perceived by the original investigators to be the best estimate of pollinator-mediated selection.

ANALYSES

MEAN-STANDARDIZED SELECTION GRADIENTS

I considered mean-standardized selection gradients ($\beta_{\mu} = \beta\mu$, where $\mu$ is the trait mean), because these are interpretable as the change in relative fitness per proportional (percent) change in the trait (Hereford et al. 2004). Because almost all selection estimates are reported as variance-standardized selection gradients (selection intensities, $\beta_{\sigma} = \beta\sigma$, where $\sigma$ is the trait standard deviation), I used reported trait means and standard deviations to translate between variance-standardized and mean-standardized selection gradients ($\beta_{\mu} = \beta_{\sigma} \mu/\sigma^2$).

MEDIAN STRENGTH OF SELECTION

To assess the typical strength of selection, I computed the median absolute value of the selection gradients (i.e. median $|\beta_{\mu}|$). To account for the upward bias in mean magnitudes due to estimation error in the individual selection estimates, I corrected each absolute selection gradient by subtracting the expected bias computed using equations 7 and 8 in Hereford et al. (2004).

ASSESSING VARIATION IN SELECTION

To assess variation in selection in space (among sites within a year) and time (among years at a site), I computed a measure of variation in selection that accounts for estimation errors in the gradients by subtracting the mean sampling variance from the observed among-study variance (Albertsen et al. 2021):

$$\sigma^2_{\beta} = \sqrt{\sigma^2_{\beta} - \text{SE}_{\beta}^2}$$

where $\sigma^2_{\beta}$ is the variance of the selection-gradient estimates among studies, and $\text{SE}_{\beta}$ is the sampling variance of each selection-gradient estimate. I expressed the corrected variance as a standard deviation to facilitate interpretation. For mean-standardized selection gradients, this measure can be interpreted as the mean dispersion of the selection estimates in units of the strength of selection on fitness itself.
While accounting for sampling errors can also be done in a formal meta-analysis (e.g. Morrissey 2016), I considered the present dataset too small for making such an analysis meaningful.

RESULTS

Selection on traits functionally related to pollination is often moderately strong (median $|\beta|$ = 0.51, bias-corrected median $|\beta|$ = 0.40, $n = 396$), and can be very strong ($\beta >> 1$) in specific cases (Fig. S1).

Comparing estimates of net selection (considering open-pollinated plants only) and pollinator-mediated selection (as estimated by subtracting selection gradients estimated for hand-pollinated control plants) reveals that selection on plant size and floral display is often mediated only partly by pollinators (Table S1, Fig. S2). In contrast, selection on fit traits and flower size is often mediated primarily by pollinators.

<table>
<thead>
<tr>
<th>Trait group</th>
<th>$\beta_{\text{net}}$</th>
<th>$\beta_{\text{pollinators}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Display</td>
<td>1.04 (44)</td>
<td>0.35 (38)</td>
</tr>
<tr>
<td>Fit</td>
<td>0.68 (94)</td>
<td>0.83 (33)</td>
</tr>
<tr>
<td>Flower size</td>
<td>0.36 (38)</td>
<td>0.37 (34)</td>
</tr>
<tr>
<td>Plant size</td>
<td>0.46 (33)</td>
<td>0.25 (35)</td>
</tr>
</tbody>
</table>

Table S1. Median strength of selection (mean-standardized selection gradients) on trait functional classes when estimated for open-pollinated plants ($\beta_{\text{net}}$), and as the difference between selection on open-pollinated and hand-pollinated plants ($\beta_{\text{pollinators}}$). Sample sizes are given in parentheses.
Selection tended to be stronger on display traits (e.g. number of flowers) and fit traits (e.g. spur length), and weaker on herkogamy (anther-stigma separation) and reward traits (Fig. S3).

Selection estimates are usually associated with considerable uncertainty. The median strength of selection of 51% of the strength of selection on fitness is only a little larger than the median standard error of the estimates (±37.4%). Consequently, in any given study, most selection-gradient estimates are statistically non-significant. If we set $|\beta_{\mu}|>1.96 \times SE(\beta_{\mu})$ as a criterion for statistical significance, 28.9% of the estimates would be declared significant.

The relationship between mean- and variance-standardized gradients depends on the phenotypic coefficient of variation (CV). In the case of flowers, it is particularly interesting to note that fit traits tend to have lower proportional variances than other traits. This pattern has important consequences for interpreting patterns of selection (Fig. S3) because the mean-scaled gradient corresponding to a given variance-scaled gradient will tend to be higher for fit traits than for other traits.

**Figure S3.** Scatterplot of absolute mean-standardized and variance-standardized multivariate selection gradients on plant traits, with colors representing distinct trait functional groups. Variance-standardized gradients describe the change in relative fitness per standard deviation change in the trait, and mean-standardized gradients describe the change in relative fitness per change in the trait mean, with a value of 1 corresponding to the strength of selection on relative fitness as a trait. Dotted lines illustrate how the relationship between variance-scaled and mean-scaled gradients vary with the coefficient of variation (CV) of the trait. The black dots represent three hypothetical traits which rank opposite for the two measures of selection strength, with variance-standardized gradients of 0.2, 0.3 and 0.4 corresponding to mean-standardized gradients of 2, 1.2, and 0.8. (B) Distribution of mean-standardized selection gradients across trait functional groups.

**Figure S2.** Comparison of mean-standardized selection gradients for four trait functional classes when estimated for open-pollinated plants ($\beta_{\text{net}}$), and as the difference between selection on open-pollinated and hand-pollinated plants ($\beta_{\text{pollinators}}$). Data are the same as shown in Table S1.
Spatial and Temporal Variation

Variation in selection in space and time can be substantial even after accounting for sampling error (Fig. S4). The observed variation in selection exceeded the mean sampling variance in 52.9% of the cases for temporal variation ($n = 51$), and 46.3% of the cases for spatial variation ($n = 54$). For those cases where the observed variation in selection exceeded the mean sampling variance, the median dispersion of the estimates was 25.2% for temporal variation, and 26.4% for spatial variation.

Figure S4. Patterns of temporal (among sites within a year) and spatial (among years for a site) variation in phenotypic selection on pollination traits. The barplots indicate the proportion of cases where variation in selection remain after accounting for sampling variance, and the boxplots give the distribution of error-corrected standard deviations of selection gradients for those cases where variation was detected. The error-corrected standard deviations can be interpreted as the average difference in selection among years (for temporal variation) or sites (for spatial variation). A mean-standardized selection gradient of 100% means that selection is as strong as selection on fitness as a trait.
REFERENCES


REFERENCES FOR STUDIES INCLUDED IN THE DATABASE


