Longitudinal and cross-sectional selection on flowering traits in a self-incompatible annual.

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Abstract

Net selection on a trait reflects the association of phenotype to fitness, across an entire life cycle. This longitudinal estimate of selection can be viewed as the summation of selection episodes, each characterized by a cross-sectional estimate. Selection may be consistent in direction and strength across episodes for some traits, fluctuating in others, and for some, concentrated in a single intense event. Additionally, while selection on plant reproductive traits is predicted to be stronger through male fitness than female fitness, male fitness remains less studied. We investigated how selection on flowering traits in *Brassica rapa* varied temporally and spatially by measuring male reproductive fitness in four experimental populations with two spatial arrangements. To estimate longitudinal and cross-sectional selection, we introduced male-sterile plants at successive intervals. We genotyped over 3000 plants and calculated selection on flowering time, duration, and total flowers. Cross-sectional analyses revealed directional selection was common, but patterns were masked by longitudinal estimates. Comparing selection gradients and coefficients revealed conflicting selection directions, suggesting the importance of trait correlations in selection estimates. Spatial population arrangement significantly impacted pollen movement and the strength of selection, demonstrating how breeding timing, spatial aggregation, and male fitness interact to create complex evolutionary dynamics.

Keywords

gene traps, male fitness, selection, Brassica rapa, flowering time, trait variation

Introduction

Unlike many animal species with highly synchronized breeding periods lasting only days or hours (Fogarty et al., 2012; McDiarmid, 1994; Schreiber & Burger, 2001; Urquhart, 1960), most flowering plants deploy reproductive structures sequentially over weeks or even months. Pollen transfer from donor to recipient is largely passive, mediated by biotic or abiotic vectors whose effectiveness fluctuates with environmental conditions (Ackerman, 2000; Elzinga et al., 2007; Polatto et al., 2014). Consequently, a plant's reproductive success represents the sum of all day-to-day mating events within an entire breeding season. The association between trait values and realized mating (i.e., the direction and magnitude of selection on plant traits), could in theory vary across dates. However, many studies cannot evaluate reproductive success on such a fine scale. To address this limitation, we focus on the temporal scheduling of flower deployment and its impact on male reproductive success through pollen export over the entire breeding season. By dissecting the breeding season into discrete temporal windows, we can analyze how selection on male function varies day-to-day within a season, revealing how phenological traits shape reproductive outcomes across the flowering season.

Within-season variation in selection is most effectively demonstrated by cross-sectional selection analyses, which measure selection on a subset of the population at a particular point in time (Endler, 1986; Kingsolver et al., 2001). While longitudinal selection studies reveal the net direction and intensity of selection by measuring the relationship between phenotype and lifetime fitness proxies, the cross-sectional approach can illuminate the mechanistic underpinnings of differential survival, mating, and reproduction throughout a breeding season, i.e., the *drivers* of longitudinal selection. Comparing these approaches allows us to determine whether longitudinal selection arises through steady and consistent selection across an entire season or from a few intense selection events at specific timepoints. Understanding how selection varies across shorter, episodic temporal scales can provide critical insights into trait

evolution (Cockburn et al., 2008; Hoekstra et al., 2001; Losos et al., 2006; Walsh & Blows, 2009).

Natural fluctuations across a breeding season in population density of mates, competitors, predators, and mutualists could give rise to within-season variation in the direction or magnitude of cross-sectional selection. Such temporally variable spatial structures can influence selection patterns, as documented in animal systems (Daupagne et al., 2023; Gyulavári et al., 2017; Kasumovic et al., 2008; Punzalan et al., 2010; Wacker et al., 2014) and less frequently in plant systems (Parachnowitsch et al., 2012; Parachnowitsch & Caruso, 2008). In flowering plants, density-dependent selection can be mediated by multiple, non-exclusive mechanisms. For instance, the density of competitors influences selection in flowering plants as competition for pollinators can arise when there is temporal overlap with blooms of competing species (Flanagan et al., 2011; Landry, 2013; Levin & Anderson, 1970; Richardson et al., 2021). Besides competitors, within-season variation in the pollinator community itself (composition, abundance, effectiveness) can influence selection (CaraDonna et al., 2017; Fisogni et al., 2016; Ison et al., 2018). Finally, population-level flowering density varies as plants enter and exit the flowering season and the individual-level floral display size rises and falls over time, both of which affect both within-species and within-individual competition patterns for resources (e.g. (Austen et al., 2015; Feldman, 2008; Grindeland et al., 2005; Makino et al., 2007; Thomson, 1980)). If male fitness (seed siring success) is limited by access to mates, we might expect selection through male fitness to be particularly vulnerable to within-season changes in conspecific density and pollinator service.

Despite the importance of male fitness components, our understanding of selection in plants is heavily biased toward female fitness, as measuring seeds produced is more straightforward than determining the paternity of seeds sired. This bias was illustrated in a meta-analysis of

selection flowering time, where only 5.7% (5/87) of studies evaluated selection via male fitness (Munguía-Rosas et al., 2011). Because female fitness depends on resources and male fitness depends on mate opportunity (Bateman & Innes, 1948), there may be a disagreement among selection estimates depending on the fitness input (Conner et al., 1996; Delph & Ashman, 2006; Hou et al., 2024; Tsuji et al., 2020). When male and female fitness optima for the same trait differ, evolutionary outcomes could lead to sexually antagonistic selection, which may stifle the opportunity for the population to reach the optimal trait value for either sex (H. Wang et al., 2021).

Consider how components of the flowering schedule such as flowering onset, duration, and total flower production shape male fitness outcomes. Variability in schedule can affect population-level synchrony, influencing both mate availability and mating frequency (Augspurger, 1983; Devaux & Lande, 2010; Fox, 2003; Weis et al., 2005). When flowering schedules vary among individuals, plants enter and exit their reproductive phase asynchronously, creating a dynamic environment in which selection acts. To illustrate our conceptual framework, we imagine two hypothetical scenarios relating variation in these flowering traits and selection (**Fig. 1**). In scenario 1 (**Fig. 1A**), flowering time (early, mid, or late) is uncorrelated with (or positively covaries with) duration or total number of flowers. Thus, selection through male fitness favors early flowering onset early in the season, and late flowering onset at the end. This shift in selection is driven entirely by which plants are in flower. In scenario 2 (**Fig. 1B**), duration and total flowers negatively covary with flowering time, thus early flowering plants have the longest duration of flowering. In this case, early flowering plants maintain presence throughout the season, but selection could weaken over time as more plants enter the mating pool. Note that these scenarios assume no variation in per-flower pollinator service across the season. A decline in per-flower transfer in any one of the three depicted intervals would diminish the contribution of that episode to net selection. Temporal variation in factors affecting pollen

transfer and correlations between these factors can create heterogeneous selection pressures across the flowering season. This raises the possibility of selection shifting in direction and intensity on flowering traits within a flowering season.

One difficulty in estimating selection on the flowering schedule through the pollen-export fitness component arises when female qualities vary across time. Pollen export is intrinsically a trait of the donor but must be quantified through the number of seeds sired. This poses no problem if all females are of equal and constant quality, i.e., invariant in the probability that pollen receipt results in offspring production. However, flowers produced toward the end of the flowering season typically have reduced fruit maturation rates (Austen et al., 2015; Weis & Kossler, 2004). This decline can stem from priority effects: early flowers access the full pool of maternal resources, which become progressively depleted for later blooming flowers. The “gene-trap” method developed by Devaux & Lande (2010) and refined by Ison & Weis (2017) can help circumvent the priority effect bias. This approach involves introducing successive batches of genetically-uniform pollen-recipient plants– all at identical developmental stages– into the experimental population, followed by paternity analysis of their seeds. By controlling for variation among pollen recipients, this method reveals the strictly male component of selection through analysis of covariance between donor traits and siring success.

Research goals

In this study, we investigate how selection via male fitness on flowering schedule components – flowering time, flowering duration, and total flower production– varies throughout the breeding season in *Brassica rapa* through the gene-trap method. Our primary research goal is to evaluate if selection gradients measured across the entire season (longitudinal selection) emerge from consistent selection or from episodic bursts of selection (cross-sectional selection). We extend this goal by also examining if the longitudinal and cross-sectional selection estimates vary

171 based on the spatial arrangement of plants within a population. Another research goal is to
172 quantify if trait correlations create conflicts between direct and total selection. Lastly, to
173 contextualize effects of spatial arrangement, we examine how changes to plant spatial
174 arrangement affect the distances pollen travels to fertilize seeds. By comparing selection at
175 different temporal scales and spatial contexts, we aim to better understand the evolutionary
176 dynamics shaping flowering traits. This integrated approach provides insights into the basic
177 evolutionary processes shaping flowering traits and contributes to our knowledge of how
178 selection operates on reproductive traits in plant populations.
179

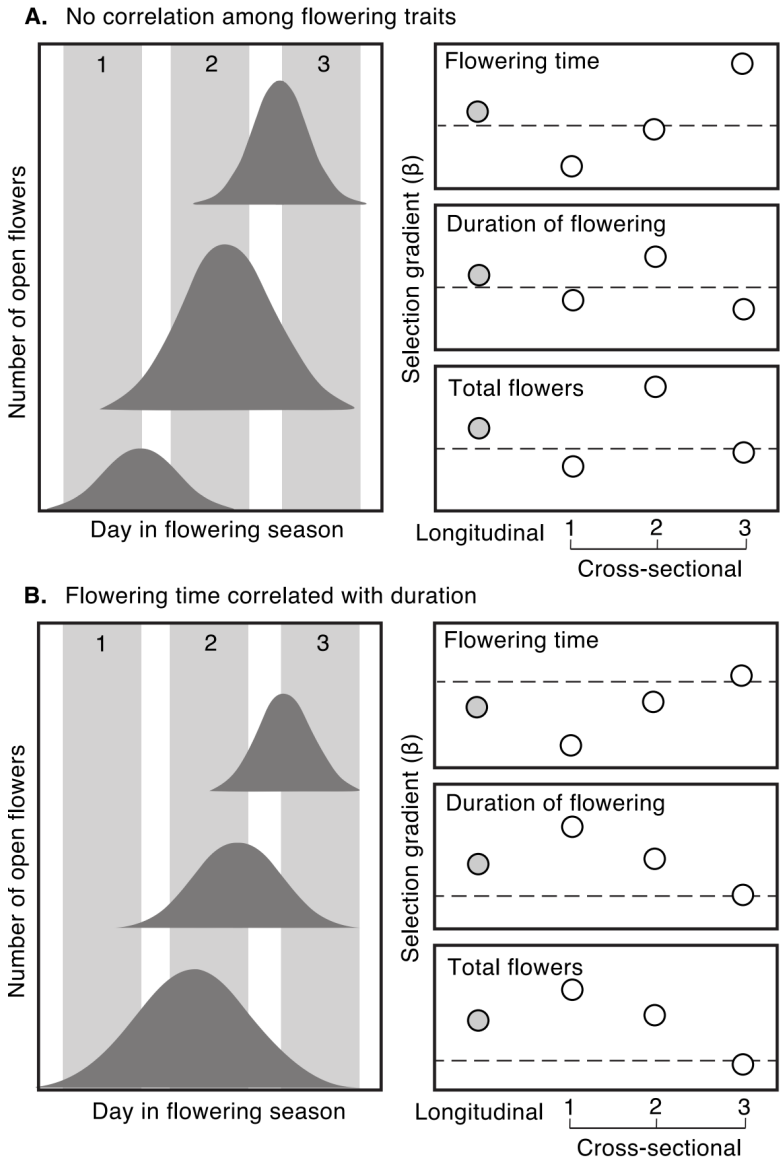

Figure 1. Conceptual diagram illustrating how selection on flowering traits (flowering time, duration, and total flowers) varies temporally across a breeding season and how cross-sectional and longitudinal selection estimates relate. Each bell curve represents an individual plant's flowering distribution. **(A)** When flowering traits are uncorrelated, selection pressures shift throughout the season. The population's flowering distribution (left) shows distinct patterns across three time intervals (grey bars). Selection gradients (circles) show direction and magnitude of selection with their position relative to zero indicating selection for increases or decreases in the trait value. Selection gradients measured at these cross-sectional time points reveal how discrete episodes of selection contribute to overall longitudinal selection pattern (right). Since pollen from each individual dominates in their corresponding interval (e.g. pollen from early-flowering individuals in interval 1) this results in weak longitudinal selection when averaged across the season. **(B)** When first flower timing correlates negatively with duration and total flowers, early-flowering individuals also flower longer and produce more flowers. Thus, the

first to flower dominate the pollen pool in interval 1 and 2, but early, intermediate, and late flowering individuals are all equally represented in the pollen pool during interval 3. This correlation creates strong selection patterns across intervals 1 and 2, which drive strong longitudinal selection on all three flowering traits.

Methods

Study species: *Brassica rapa*

Brassica rapa is a non-clonal annual in the Brassicaceae. The species is native to Eurasia but is naturalized throughout much of North America (Gulden et al., 2008). Flowers are typically perfect (containing both pollen-producing, and ovule-producing, structures within the same flower), and a plant begins flowering 30-60 days after seed germination (Austen & Weis, 2016a; Ison & Weis, 2017). The inflorescence is an elongated raceme, and flowers will persist for one to three days but senesce more quickly once fertilized. Flowering can continue through the fruit set of the earliest flower (Austen & Weis, 2016a). *B. rapa* is an obligate out-crosser with a sporophytic self-incompatibility system (Bateman, 1955; Murase et al., 2020). Insect pollinators include generalist bee and fly pollinators in the Apidae, Halictidae, and Syrphidae, and butterflies in the Lepidoptera.

Experimental design

Field populations

We established four perfect-flowered experimental populations of *B. rapa* at the University of Toronto's Koffler Scientific Reserve (44°1′N, 079°32′W) during summer 2011 using seeds bulk-collected from Eastern Quebec in 2009 (Austen & Weis, 2016a). Two populations flowered from July 4 – Aug 11 ("early season"), and two flowered from Aug 16 – Oct 13 ("late season"). The inclusion of these two flowering periods allowed us to capture any possible changes in pollinator service (or other ecological factors) across a larger temporal range.

The two populations within each of the early- and late-season treatments differed in spatial arrangement (one "clumped" and one "even"). Both spatial arrangements consisted of a hexagonal grid with 4 m sides. In the even populations, plants were evenly spaced at 0.5 m apart (211 total plants; **Fig. 2A**). The clumped populations had six small hexagons within a

249 larger hexagon, with small hexagons 2.7 m apart and plants within the small hexagons 0.17 m
250 apart (216 total plants; **Fig. 2B**). In total, our design included four distinct experimental
251 populations (i.e. even early season, clumped early season, even late season, clumped late
252 season).
253
254 *Gene-trap implementation*
255 To assess male fitness and pollen movement, male sterile plants ("gene-traps") were deployed
256 as standardized pollen recipients. These male-sterile plants were produced by back-crossing
257 Wisconsin FastPlants line 1-107 (carrying male sterility) into the Eastern Quebec population
258 background (see Ison & Weis 2017: "constructing the gene trap line"). This breeding approach
259 yielded functionally female plants that were morphologically and developmentally similar to the
260 perfect-flowered plants while maintaining male sterility.
261
262 Each population contained six gene-trap positions where male-sterile plants were placed. These
263 positions were evenly spaced in the even populations and positioned at the center of each small
264 hexagon in the clumped populations (**Fig. 2**). Gene-trap plants were systematically replaced
265 approximately 3-5 days throughout the flowering season (**Fig. 2** and **Table S1**). The temporal
266 rotation of new male-sterile plants as pollen recipients at each interval eliminated variance in
267 mate quality available to prospective sires across the season, ensuring our selection estimates
268 reflected differences in the competitive abilities of the perfect-flowered pollen plants as pollen
269 donors. Seeds produced by these standardized maternal plants were later genotyped to
270 estimate siring success of the perfect-flowered pollen donors through paternity analysis.
271
272 ***Phenotypic measurements and genetic analysis***
273 We recorded three flowering traits for each pollen-donor (854 perfect-flowered plants): day of
274 first flowering (flowering time), flowering duration, and the total number of fresh flowers

275 (summed across census days). Prior to analysis, we standardized all phenotypes by z-scoring
276 them within each of the four populations.
277
278 We collected tissue samples from all perfect-flowered plants (potential sires) and each gene-
279 trap plant (264 maternal plants; 42 per early-season populations and 48 per late-season
280 populations). During winter 2011-12, we germinated and grew gene-trap offspring in a
281 greenhouse (see Ison and Weis 2017 for methods). For this study, we aimed for twelve
282 offspring per gene-trap plant, but some gene-trap plants produced fewer than twelve viable
283 seeds and for a few gene-trap plants, we sampled more than twelve offspring (mean 10.9; 1970
284 total offspring; **Table S1**). Offspring were tissue sampled when at least two true leaves were
285 present. Leaf tissue from parents and offspring was dried in silica gel.
286
287 *Genotyping methods*
288 We extracted DNA from the dried tissue samples using isopropanol precipitation methods
289 (Rogers et al., 1996). We characterized the plants' DNA at ten *B. rapa* microsatellite loci (Lowe
290 et al., 2004; Suwabe et al., 2002) (for primer information, see **Table S2**). We conducted 10 µl
291 polymerase chain reactions with 1 µl of DNA template, 5 µl of GoTaq Colorless MasterMix
292 (Promega), 0.5 µl of BSA, 0.25 µl of additional $MgCl_2$, 0.16 µl M13-tagged fluorescent dye (ABI
293 dye set-33), 0.05 µl of forward primer with M13 tail, 0.6 µl reverse primer, and DNase free water
294 to volume. Each PCR consisted of a 3 min 94°C denaturing cycle followed by 30-32 cycles of 30
295 s at 94°C, 30 s at annealing temperature (see **Table S2**), and a 30 s extension step at 72°C.
296 Three additional cycles were run with an annealing temperature of 55°C followed by a final 10
297 min 72°C extension step. We sent the PCR products to the University of Toronto's Center for
298 Analysis of Genome Evolution and Function for capillary gel fragment analysis. We scored the
299 resulting genotypes using Peak Scanner version 1.0 (Biosystems, 2006). To calculate
300 genotyping error, we repeated the PCR, fragment analysis on 96 haphazardly selected

samples. We calculated both the allelic dropout error rate, ε1, and the stochastic error rates due to typing error, ε2, which can be attributed to mutation, miscalling, polymerase error, and data entry error (J. Wang, 2004).

Paternity Analysis/ MCMC Model

We conducted analyses using R 4.4.0 (R Development Core Team 2024). We assigned proportional paternity, reconstructed pedigrees, and checked for convergence using MasterBayes and coda for analysis (Hadfield, 2017; Plummer, 2024). MasterBayes uses Bayesian statistics to find the maximum likelihood of paternity through the calculation of a posterior distribution relying on both genetic and phenotypic data to find the highest probability offspring-paternal pair (Hadfield, 2017; Jones et al., 2010). The statistical inference employs a Bayesian probabilistic architecture to simultaneously derive posterior probability distributions across 1) genealogical relationships represented in the pedigree structure *P, and* 2) the coefficient vector β that parametrizes the log-linear model incorporating non-genetic covariates. This joint estimation process integrates the uncertainty in both the familial relationships and the magnitude of non-genetic effects within a unified probabilistic framework. The non-genetic information that is an input of the model comes out as the multinomial log-linear model. The coefficients from the multinomial log-linear model are analogous to the coefficient of a multiple regression, thus the coefficient derived on non-genetic data from paternity assignment of offspring outputs a selection gradient as conducted in (Austen & Weis, 2016a) with the R package MasterBayes (Hadfield et al., 2006).

To parameterize our model, we initialized three independent MCMC chains with differing starting conditions. The first two chains were initialized with fixed genotyping error rates (*e1* and *e2*) and allele frequencies, while the third chain incorporated normally distributed random starting values for the beta coefficients, with a mean vector of [-0.1,0.1] and a standard

327 deviation of 0.05. We optimized MCMC sampling using a tuning parameter of 0.325 to achieve
328 acceptance rates between 20% and 50%. Each chain was run for 110,000 iterations with a
329 burn-in period of 10,000 iterations. To reduce autocorrelation, we employed a thinning interval
330 of 100, resulting in 1,000 store iterations per chain. The chains were run with a maximum
331 mismatch tolerance of 5. This multi-chain approach with different initialization parameters
332 allowed us to assess convergence and mixing of the MCMC sampling while accounting for
333 potential genotyping errors in the pedigree reconstruction. We tested all chains for convergence
334 using the Gelman-Rubin Diagnostic using the coda package (Plummer et al., 2006), and
335 removed all models from the analysis that did not reach convergence (convergence is indicated
336 by values lying between 0.9-1.1).
337
338 ***Selection analysis framework***
339 *Measuring longitudinal and cross-sectional selection*
340 We estimate selection gradients (β) on our phenotypes for each interval (cross-section) and for
341 the entire season (longitudinal). Longitudinal selection gradients simply evaluated selection
342 based on all offspring generated within each of the four populations. For the cross-sectional
343 approach, we estimated selection in discrete intervals across the flowering season by
344 implementing the same analytical framework as with longitudinal selection, but we restricted the
345 pollen pool to specific windows when a single batch of gene-trap plants were present in the field
346 (7 intervals for early season and 8 intervals for late season; **Table S1**). Here, potential sires
347 were limited to plants producing pollen during the active gene-trap interval and thus plants that
348 were non-flowering were removed from the interval-specific analysis. To account for temporal
349 variation in pollen availability, we randomly subsampled offspring proportionally to each time
350 period's contribution to the total seasonal pollen pool. This approach generated interval-specific
351 selection gradients that revealed how selection pressures shifted throughout the flowering
352 season.

Comparing multivariate and univariate models

Our multivariate selection framework had incorporated all three flowering traits (flowering time, flowering duration, and total flower number) simultaneously into the log-linear model, providing an estimate of direct selection on the focal trait. This multivariate approach disentangles the network of trait relationships, allowing us to isolate the direct selection acting on each trait while statistically controlling for the influence of correlated traits. Thus, the multivariate selection model partitions the shared variance of traits to reveal which traits are directly under selection versus those that change due to correlated responses. However, we also measured selection using a univariate model where only the trait of interest was incorporated into the log-linear model, providing a selection differential and a measure of total selection. Selection differentials capture the total selective pressures acting on each trait, including both direct selection on the trait itself and indirect selection arising from correlations with other traits because covariation with other traits is not included in the univariate model. This univariate selection model reflects the net selection on each trait in natural conditions.

We identified traits experiencing selective conflicts by comparing the directionality of direct (β) and total (S) selection estimates. Traits exhibiting opposing signs between β and S were classified as being in “conflict zones,” indicating that their evolutionary trajectory is constrained by antagonistic selection pressures mediated through trait correlations (Ruffley et al., 2023). The comparison reveals how trait covariation can modify the adaptive landscape and potentially constrain evolutionary responses.

Distance of pollen movement analysis

The log-linear model framework allows for the incorporation of spatial effects through pairwise distances between maternal plants and potential sires. The spatial effect coefficient (β) from the

posterior distribution quantifies the decay in mating probability with increasing distance and follows an exponential decay function (Exponential decay = $e^{\beta * x}$, where β is the peak of the posterior distribution and *x* is the pairwise distance).

The spatial component was incorporated directly into the multinomial log-linear model with MasterBayes. The exponential decay model provides a mechanistic understanding of pollen movement where negative β values indicate decreasing probability of successful mating with increasing distance between pairs of plants.

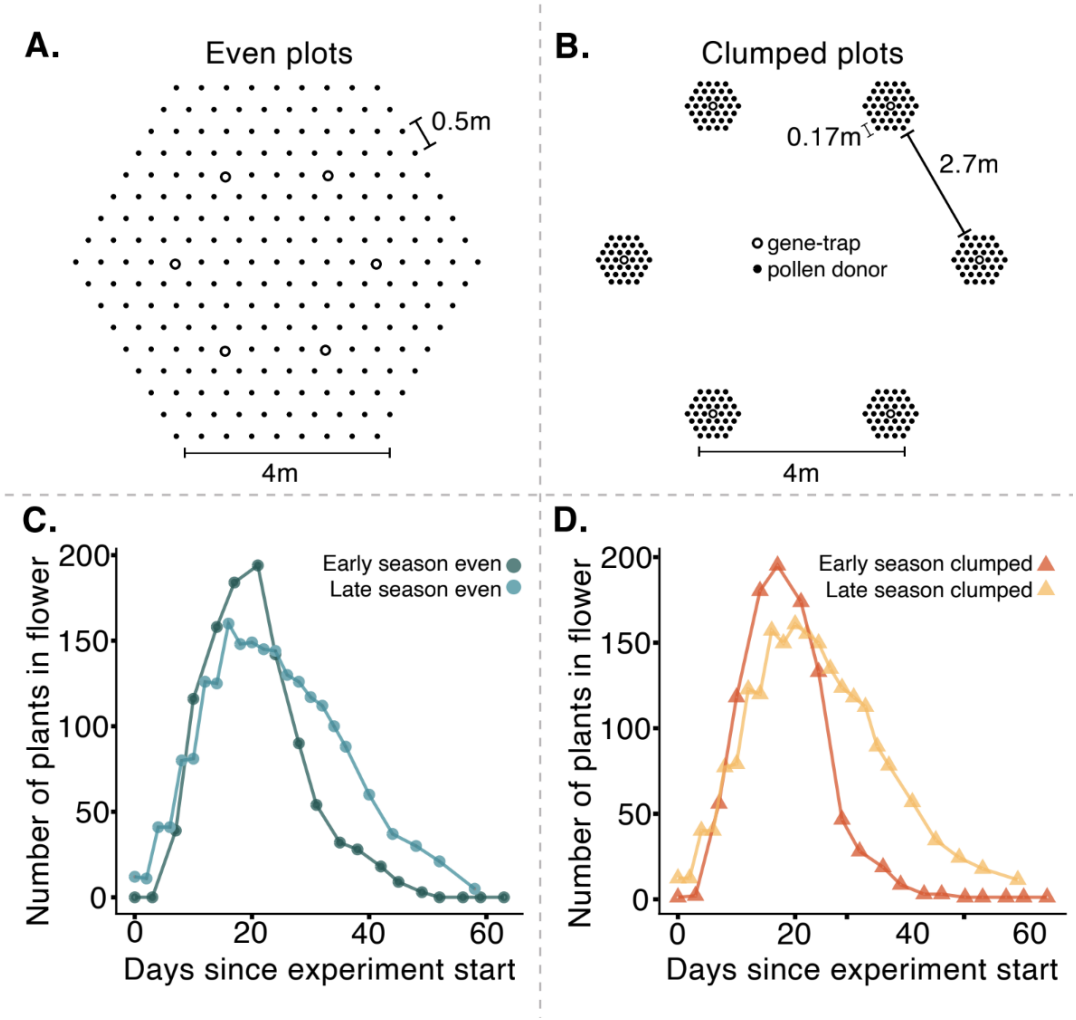

Figure 2. Diagrams of the experimental population spatial arrangements and flowering phenology. Populations were hexagonal in shape and each side was 4 m long. Each population had six gene-trap (male-sterile plants) positions denoted by an open circle **(A&B)**. Gene-trap plants were added and removed from populations in consecutive batches every 3-5 days throughout the experiment (7 batches for July-Aug time period, and 8 batches for Aug-Oct time period, see **Table S1** for placement schedule). For the even spatial arrangement **(A)** plants were spaced 0.5 m apart. In the clumped arrangement **(B)** there were six smaller hexagons at the corner of each of the population hexagons. Within each smaller hexagon plants were 0.17 m apart and smaller hexagons were 2.7 m from each other. Flower counts were recorded for all plants on census days corresponding to each data point shown in the flowering phenology curve **(C&D)**. The even populations are denoted by circles and the clumped populations are denoted by triangles. Dark blue and orange colors indicate the experiment was conducted in the early season (July-Aug) and the light blue and yellow colors indicate the experiment was conducted in the late season (Aug-Oct).

Results

We successfully genotyped nearly all populations (n=854), gene-trap (n=264), and offspring (n=1970) plants at the 10 microsatellite loci. There was 3.7%, 3.8%, and 2.5% of the genotypic data missing across loci, for population, gene-trap, and offspring plants, respectively. For the paternity analysis, we tested convergence of our three chains per analysis. In total, across direct and total selection and cross-sectional and longitudinal estimates in the four populations, we ran 242 chains, and 238 of them converged (98.3%). Analyses that did not reach convergence with the Gelman-Rubin Diagnostic were removed from the results.

Longitudinal selection on flowering traits via male fitness

Selection varied among populations and traits when measured across the entire flowering season. One population (clumped, late season) showed significant directional selection favoring late flowering, while the remaining populations did not show significant evidence of selection on flowering time (**Fig. 2A**). We observed significant selection for longer flowering duration in both late season populations but no significant selection in early season populations (**Fig. 2B**). Selection favored more total flowers in three populations, with only the early season clumped population having no significant selection (**Fig. 2C**).

Cross-sectional selection on flowering traits via male fitness

Cross-sectional selection analysis using the gene-trap sampling periods revealed dynamic patterns of selection that varied both temporally and spatially. All populations showed temporal shifts in selection on flowering time, generally favoring early flowering at the beginning of the season and late flowering towards the end, with non-significant estimates during mid-season (**Fig 2A**). Notably, cross-sectional selection gradients on flowering time had the largest estimated magnitudes in early and late flowering plants in both experiment timings in clumped populations (flowering time β = -0.37± 0.098 through 0.56 ±0.105, duration β = -0.28 ±0.048

through 0.48 ±0.112, total flowers β = -0.03 ± 0.0166 through 0.03 ± 0.009; **Fig. 2**). There were two trend-breaking anomalies in the final gene-trap sampling period: the late season even population had directional selection for early flowering (β = -0.07 ± 0.040), while the early season clumped population had no significant selection.

Cross-sectional selection on flowering duration and total flowers varied based on the population spatial arrangements. Both spatial arrangements had modest selection for longer flowering duration in many of the gene-trap intervals (13 intervals) with strong selection in late flowering plants (clumped late season β =0.48 ±0.112, **Fig. 2B**). The even populations had relatively consistent selection for more total flowers throughout the season (mean β =0.15, max β = 0.022, min β = 0.012, **Fig. 2C**). In contrast, the clumped populations exhibited selection for shorter flowering duration (β = -0.28 ± 0.074 and β = -0.11 ± 0.048) and fewer total flowers (β = -0.05 ± 0.0165) during early and mid-season (**Fig. 2B&C, Table S3**).

Conflicts in total and direct selection

While longitudinal analyses revealed no clear conflicts between direct and total selection (**Fig. S1 and Table S3**), cross-sectional analyses uncovered temporal variation in selection conflicts (**Fig. 4 and Table S3**). The late season clumped population showed discordance between direct selection favoring late flowering and no total selection on flowering time (β = 0.02 ± 0.015, S = 0.001 ± 0.0154, **Fig. S1A**). Measurements from early flowering plants in the late season even population revealed conflict in both duration (β = 0.04 ± 0.016 S = -0.023 ± 0.019, **Fig. 4B**) and total flowers (β = 0.01 ± 0.010, S = -0.02 ± 0.009 (**Fig. 4C**), where direct and total selection opposed each other in sign. Additionally, gene-trap sample periods showed varying degrees of conflict between direct and total selection, though not always reaching statistical significance.

Pollen movement in differing spatial arrangements

Pollen movement patterns varied with both spatial arrangement and gene-trap sampling periods. Clumped populations generally showed greater pollen dispersal distances than even populations across the season (**Fig. 5A** and **Table S4**). The gene-trap sample periods revealed that the even populations had more variance in pollen movement distances with the shortest pollen movement distance being during peak flowering time ($\beta = -1.74 \pm 0.232$ in early season and $\beta = -1.104 \pm 0.181$ in late season), while clumped populations had a relatively consistent distance of pollen movement throughout the season (**Fig. 5B, Table S4**).

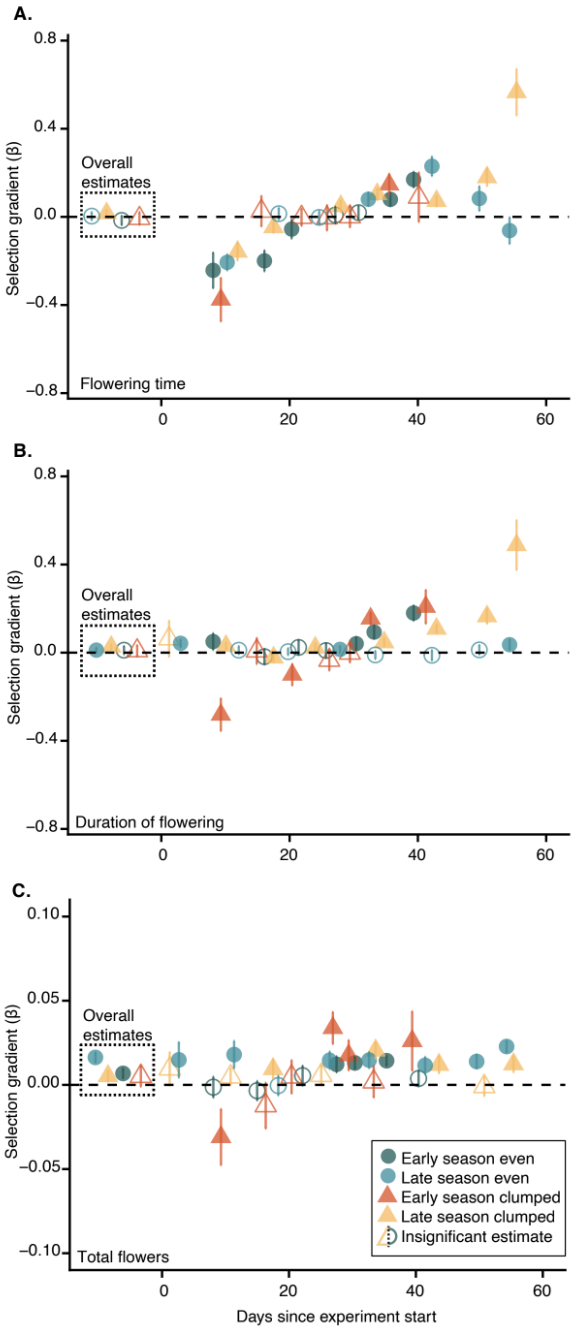

Figure 3. Longitudinal and cross-sectional estimates for selection gradients (±SE) on **(A)** flowering time, **(B)** duration of flowering, and **(C)** total flowers in four experimental populations. Longitudinal selection gradients are depicted in the dashed box, while selection gradients in each time interval correspond with the days since being placed in the field axis. Blue circles correspond to evenly spaced populations and yellow and orange triangles represent clumped populations, and the dark blue and dark orange represent the early season populations while the light blue and yellow represent the late season populations. A filled-in shape indicates the estimate and ±SE do not cross zero while an empty shape indicates the estimate and ±SE cross zero and are therefore non-significant estimates.

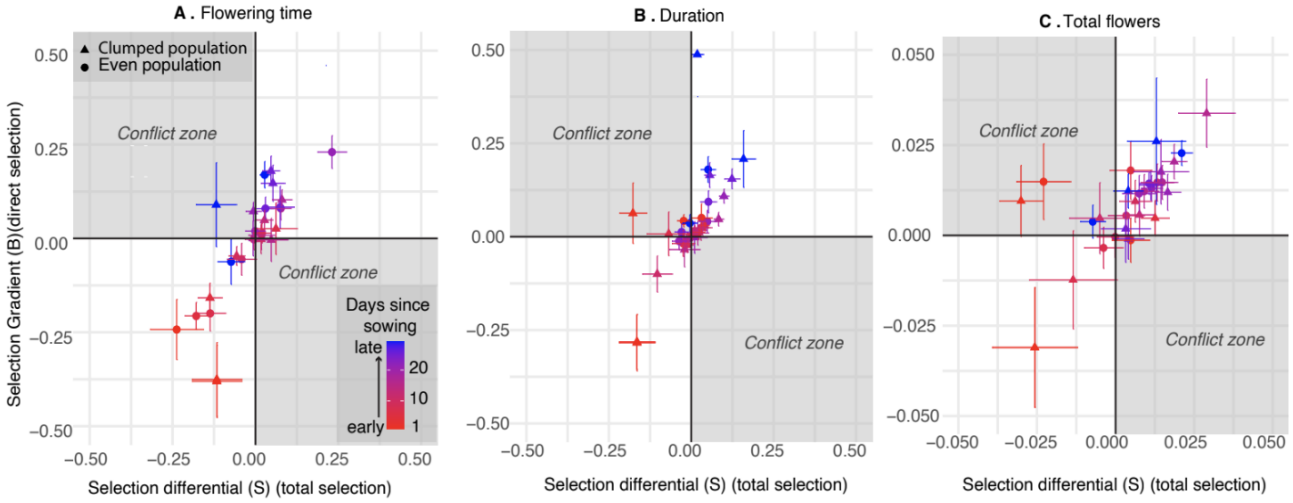

Figure 4. Direct and total cross-sectional selection plotted for the three traits: **(A)** flowering time, **(B)** duration, **(C)** total flowers. Points in grey conflict zones indicate opposing significant signs of selection estimates. Even populations are shown as circles and clumped populations are shown as triangles, and the color of the points indicates the time within the season.

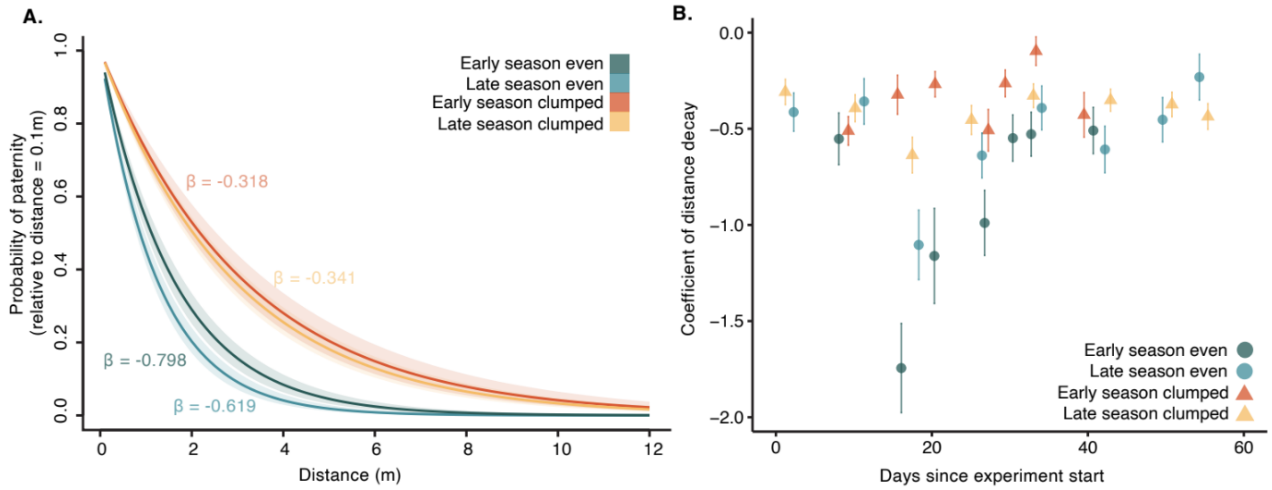

Figure 5. (A) Probability of paternity relative to distance (m) for the two population types in the early and late season experiments plotted as an exponential decay of the distance decay coefficient. Shaded regions represent 95% Bayesian Confidence Intervals. Blue colors represent even populations and yellow and orange colors represent clumped populations. **(B)** Coefficient of distance decays over cross-sections of time and plotted without exponential decay function.

Discussion

Cross-sectional selection analyses reveal mechanisms of longitudinal selection in a plant with a long-breeding season

While longitudinal analyses capture season-wide trends, examining selection at a finer temporal scale uncovered nuanced patterns that varied in both strength and direction of selection throughout the breeding season (**Fig. 3**). The overall selection on flowering time was characterized by mostly slow and steady weak selection, punctuated by bursts favoring early flowering (**Fig. 3A**). These bursts were often matched or countered by weaker selection for later flowering onset throughout the season. Early in the season, we observed strong directional selection for early flowering, as the mating pool was dominated by early-flowering individuals (**Fig. 3A**). At the beginning of the season there is limited variance in flowering start time providing less trait variation for selection to act on. As such, we expect a small magnitude of selection on early flowering– this makes the strong selection we found for early flowering surprising and suggests that there is a true advantage to being one of the first pollen producing plants, even among the early flowering cohort. This aligns in the literature with findings that the earliest flowering plants can experience reduced competition for pollinators, potentially increasing reproductive success (Elzinga et al., 2007; Kehrberger & Holzschuh, 2019).

Late in the season, we found strong directional selection for late flowering in all four experimental populations, apart from the final interval for the late-season-even population. We might expect that if early flowering plants have a long duration and continue contributing to the gene pool at the end of the season, later flowering plants may have an advantage of higher quality pollen at that time in the plant's flowering curve (Ashman & Schoen, 1994) or generally have a genetic advantage at any point in the season (Austen & Weis, 2016a). Because we found selection for late flowering plants at the end of the season and flowering time was only

negatively correlated in ~35% of the intervals with duration of flowering (~7% of intervals had positive correlations with duration and flowering time and the other ~57% of intervals had no correlation with flowering time and duration, **Table S5**), we propose that selection at the end of the season is partially due to simply the ratio of pollen available at that time but also, in the case of plants that negatively covary duration and flowering time, decreased flower quality in earlier flowering plants at the end of the season. Overall, the alternating advantages of early and late flowering through male function, combined with the likelihood that female function favors early flowering (although cross-sectional selection on flowering time via female function has to date not been evaluated empirically), suggest that there may be no net directional selection from the integration of these fitness components across the flowering season (McGlothlin, 2010; Wadgymar, Daws, et al., 2017; Wadgymar, Lowry, et al., 2017).

Our cross-sectional analysis revealed that longitudinal selection on flowering duration (which was non-significant or in the direction of longer duration, (**Fig. 3B)**) and on total flower production (which was non-significant or in the direction of more total flowers (**Fig. 3C**)) arose through steady selection throughout the season. However, in certain intervals of the early season clumped population, we observed selection favoring shorter duration and fewer total flowers, contrasting with theoretical predictions that longer flowering and more flowers would increase siring success, and thus, dampening overall season estimates (**Fig. 3B** and **C**). These patterns were temporally restricted to early and peak season days, suggesting that temporal density dependent selection was at play. At peak flowering, when there is significant overlap in flowering schedules, competition for pollinators may lead to selection pressures favoring resource conservation (Barley et al., 2022; Eisen et al., 2020). The emergence of negative or neutral selection estimates highlight that the evolution of flowering traits is contingent upon

temporal dynamics and a single event can undermine or cancel out season-wide trends, which underscores the complexity of selection operating in natural populations.

Within the cross-sectional analysis, we observed differences based on the spatial arrangements of the populations, though we do not have statistical power to test these observations. Interestingly, the strongest selection estimates for early and late flowering, shorter and longer duration, and fewer and more total flowers all occur in clumped populations. Although even population had more frequent significant selection estimates, clumped populations showed amplified directional shifts. This pattern of stronger selection in denser spatial arrangements aligns with studies demonstrating that pollinator behavior mediates density-dependent selection: floral abundance alters visitation patterns, which disproportionately rewards extreme trait values in dense groups (Caruso, 2002; Cohen et al., 2021; Kunin, 1993). For example, in *B. rapa*, high density populations exhibit fivefold stronger soft selection (rank based competition (e.g. driven by social competition)) than hard selection (environmentally based and independent of population composition) (Weis et al., 2015), with elevated Gini coefficients reflecting stark reproductive inequality– consistent with our observation of intensified selection in clumped populations. These findings suggest that spatial density amplifies pollinator-driven selection by increasing both competition for visits and variance in mating success. Future work directly linking pollinator foraging decisions to selection gradients across spatial arrangements could clarify how density shapes floral trait evolution in wild and managed populations.

Measuring longitudinal selection on flowering traits via male fitness enhances our understanding of their evolution

Flowering time

While the timing of flowering is affected by environmental conditions, studies have found a strong genetic basis for variance in flowering time (e.g. (Fox, 1990; Dorn & Mitchell-Olds, 1991; Geber & Griffen, 2003; Reed et al., 2022)) including the Quebec populations of *B. rapa* used in this study (independent narrow-sense heritability estimates of 0.506, 0.568, and 0.610 (Austen & Weis, 2016a; Ison & Weis, 2017). Despite widespread evidence for directional selection favoring early flowering via female fitness (reviewed in (Austen et al., 2017; Munguía-Rosas et al., 2011)), flowering time variation persists in natural populations. A key hypothesis posits that opposing selection through male fitness counterbalances female-driven selection, weakening net directional selection (Austen et al., 2017). If the counterbalance is present, then our previous understanding of the nature of selection on flowering time based on female fitness alone is misleading (Austen et al., 2017; Austen & Weis, 2016b). In short, variance in flowering time could be maintained because selection is not as strong when evaluating total fitness (the combination of male and female reproductive success) as when using female fitness alone.

By isolating male siring success using gene-trap plants and holding female qualities nearly constant through time, we observed no directional selection for early flowering in any population and even detected selection for later flowering in one clumped populations (**Fig. 3A**). This contrasts starkly with the strong early-flowering bias reported in female fitness studies (Austen et al., 2017; Austen & Weis, 2016b). However, it is important to note that non-gene-trap plants' female fitness (seed production) was unmeasured, limiting our ability to directly test the male-female counterbalance hypothesis. While total fitness integrates both components, our results demonstrate that male fitness alone does not reinforce early flowering, challenging assumptions based solely on female function.

Sex-specific selection can arise because male fitness is limited by mating opportunities (pollen dispersal), while female fitness is resource limited (ovule maturation) (Anthes et al., 2010;

Ashman & Morgan, 2004; Bateman & Innes, 1948; Burd & Callahan, 2000; Campbell, 1989).This divergence may explain a reduction net directional selection. However, even studies measuring both male and female fitness remain incomplete without accounting for unmeasured components (e.g. the correlation between flowering time genotype and seed variability or early-life mortality) (Wadgymar, Daws, et al., 2017; Wadgymar et al., 2024; Wadgymar, Lowry, et al., 2017). Thus, future studies should aim to integrate measurements of both pre- and post-reproductive fitness as well as try to measure total fitness through male and female fitness components to fully understand selective forces in plant populations.

Duration of flowering

Duration of flowering theoretically increases mating opportunities through male fitness by extending the period of potential pollen transfer (Austen & Weis, 2016a; Lloyd, 1980; Xu, 2024). However, longer duration could incur resource costs that create trade-offs generally (e.g., longer duration but lower quality flowers) (Ashman & Schoen, 1994) or on the male-female fitness axis (Ashman & Morgan, 2004; Zhao et al., 2020). In our experiment, the relationship between duration and fitness varied between experimental times and spatial contexts– both even spatial populations in early and late-season experimental runs showed selection for longer duration while the early-season clumped population displayed selection for shorter duration in certain intervals. These results suggest that selection on duration of flowering is not as intuitive as theoretically proposed, and that ecological context and fitness type can impact selection in unexpected ways.

Flowering duration presents a complex trait for selection analysis because of its poorly understood heritability. While duration is often correlated with heritable traits like flowering time, understanding of its own heritability is limited because there are few direct measurements in selection studies (Bhakta et al., 2017; Cheng et al., 2006; Hof et al., 1999; Williams et al., 2022).

These studies have found moderate to low heritability of duration. Because heritability is influenced by both genetic and environmental factors, the often observed correlation of flowering time with flowering duration may be environmental not genetically based (Austen & Weis, 2016b). In our populations, duration was correlated with total flowers and flowering time some but not all of the time (**Table S5**). This absence of pattern suggests that selection on duration may operate independently from selection on flowering time in this experiment.

Total flowers

Three of our four populations showed longitudinal directional selection for more total flowers, and one population showed no longitudinal selection for more total flowers (**Fig. 3C**; note the magnitude of selection is lower on this trait than in duration or flowering time). Similar to flowering duration, heritability estimates of total flowers are varied and much less common than estimates for flowering time (Drennan et al., 1986; Fogaça et al., 2012; Hof et al., 1999). In our study, total flowers are correlated with flowering time in two populations, indicating potential genetic or developmental constraints on independent evolution of these traits (**Table S5)**. We also suspect that the relationship between total flowers and male fitness is not straight forward– although producing more flowers theoretically increases opportunity for pollen dispersal, plants face resource allocation trade-offs between flower quantity and quality (Lanuza et al., 2023), as well as variation in the differences temporal distribution of flower production throughout the season (Burd, 1999).

Cross-sectional selection analyses reveal periods of conflict between direct and total selection

Our cross-sectional analysis uncovered conflicts between total (S) and direct (β) selection across flowering traits. These discrepancies– where total selection favored one trait value while direction selection was neutral or opposing– suggest indirect selection mediated by trait

correlations (e.g., pleiotropy or linkage disequilibrium). For instance, in the late-season clumped population, direct selection favored late flowering, while total selection was non-significant (**Fig. S1**), implying that indirect selection via correlated traits (e.g. duration or flower number) could constrain flowering time evolution. Similarly, in early-season even populations, total selection favored fewer flowers and shorter duration, but direct selection opposed this, favoring longer duration and more flowers. Such conflicts highlight how trait covariance can mask or redirect evolutionary trajectories, particularly when selection gradients interact with genetic architecture.

Evolutionary outcomes depend critically on the interplay between selection gradients and the G-matrix (genetic variance-covariance matrix). For example, in *Lobelia siphilitica*, multivariate models revealed opposing selection on flower size and number due to genetic constraints, limiting floral display evolution despite univariate selection signals (Caruso, 2004). Similarly, foundational studies by Campbell (1996) and Mitchell et al. (1998) explored genetic constraints of floral traits, highlighting how trait correlations can limit evolutionary responses. Trade-offs can be evident in life history strategies as well, as in the well-documented trade-off in *Arabidopsis thaliana* where flowering time and water use efficiency (two traits linked to different drought survival strategies) negatively covary (Kenney et al., 2014) and were found to be constrained genetically (Ruffley et al., 2023). These studies align with our findings: if traits like flowering time and duration share genetic covariance (as suggested by their correlated selection), the G-matrix could amplify or dampen responses to selection. However, the heritability of these traits– and thus the strength of constraint– remains unknown in *B. rapa* and many other plant systems. Future work estimating G-matrices alongside selection gradients in wild populations will clarify how genetic architecture mediates floral traits evolution.

Pollen moved farther in clumped populations than in even populations

726 We designed the population arrangements such that detected pollen movement via paternity
727 assignment is likely an accurate representation of how pollen moved in the populations. We
728 eliminated potential fine-scale spatial genetic structure by randomly planting pollen donor plants
729 which enabled nearly all population plants to be compatible with all maternal plants (i.e., gene-
730 traps) since they have different genetic backgrounds. Notably, we observed striking differences
731 in successful pollen movement between even and clumped spatial arrangements, where overall
732 pollen moved farther in clumped than even populations (**Fig. 5A**). When looking at the intervals
733 of time in even populations, successful pollen moved shorter distances at peak flowering time
734 and showed more seasonal variation in pollen movement distance (**Fig. 5B**). This is consistent
735 with other studies that also found longer-distance pollen movements early and late in the
736 season (Ison et al., 2014; Kitamoto et al., 2006). In contrast, pollen moved farther in clumped
737 populations, despite closer plant proximity, and maintained consistent movement distances
738 across the season (**Fig. 5B**). We observed these patterns in the distance pollen moves in space
739 in both early and late season experimental runs indicating that these patterns are robust to
740 seasonal changes in pollinator community composition, though the pollinator community stayed
741 relatively consistent between the two runs (**Fig. S2**).
742
743 While our design kept the overall number of plants constant between even and clumped
744 populations, the arrangement of the plants and density immediately around the gene traps
745 varied (50 cm in even populations and 17 cm in clumped populations). Other studies have found
746 that pollinator foraging behavior changes with plant density (Cresswell, 2000; Grindeland et al.,
747 2005; Kunin, 1997). However, how these changes in foraging behavior impacts pollen
748 movement distance is less understood. In one study, bumblebees were more likely to skip over
749 plants and their foraging had less directionality when plant density increased but that did not
750 lead to changes in pollen movement distances, based on foraging observations (Cresswell,
751 1997). In our study, we hypothesize that the dense clumped populations of individual plants

752 were hard to distinguish, and pollinations may have been making foraging decisions at a clump-
753 level, rather than an individual-plant level. In support of this, we see an elevated probability of
754 paternity at 4 m in clumped populations **(Fig. 5A**), which is of note as 4 m is the distance
755 between neighboring clumps (**Fig 2B**)–this heightened 4 m-travel in clumped populations
756 suggests that pollinators may be treating clumps as a “single plant”.
757
758 **Conclusion and future directions**
759 Our study demonstrates how multiple approaches for estimating selection can reveal complex
760 evolutionary dynamics that might otherwise remain hidden. The cross-sectional approach
761 reveals nuanced patterns of selection throughout the flowering season that were masked in
762 longitudinal estimates, highlighting the importance of temporal scales in selection studies and
763 displaying the mechanisms behind longitudinal selection estimates. By examining selection
764 through male fitness in *B. rapa*, we uncovered selection for late flowering in one of four
765 populations, which may help explain the maintenance of flowering time variation, despite
766 consistent selection for early flowering through female fitness in previous studies. While we
767 found limited evidence of conflicting selection through direct and total selection, this analytical
768 framework provides a valuable tool for identifying potential evolutionary constraints in traits with
769 stronger trade-offs or genetic relationships. Finally, spatial arrangement emerged as a key
770 factor influencing both selection strength and pollen movement patterns, demonstrating how
771 local aggregation can modify selection pressures.
772
773 Future studies should integrate both male and female fitness components to provide a
774 comprehensive view of selection acting on plants. Additionally, incorporating temporal sampling
775 designs will better capture how selection varies throughout the season, allowing for deeper
776 insight into the drivers of selection. Finally, measuring suites of potentially correlated traits offers
777 opportunities to evaluate selection conflicts and understand how genetic architecture influences

evolutionary outcomes. This multifaceted approach to studying selection will enhance our understanding of how natural populations respond to selection pressures across different spatial and temporal scales.

Data accessibility statement: *The data underlying this article are available in: (doi for dryad if manuscript is accepted).* If the reviewers would like to see the code, please have the editor reach out to the corresponding author.

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Supplementary Figures

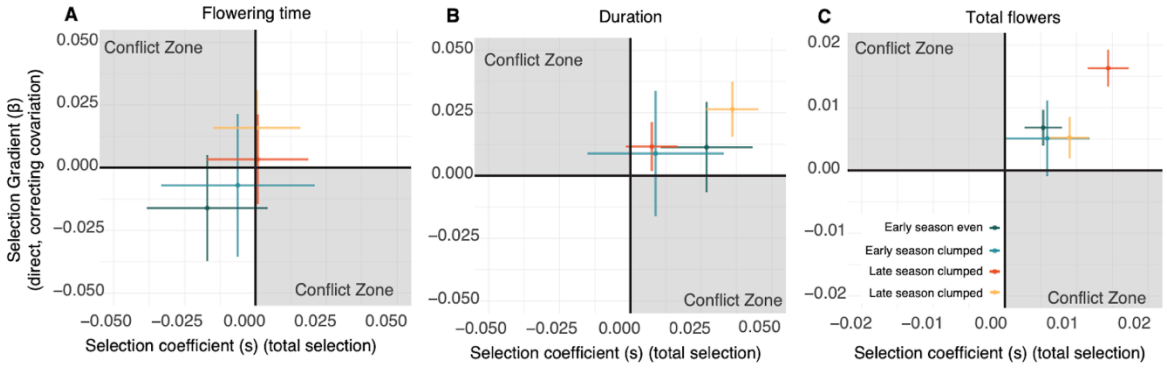

Figure S1. Overall selection conflict for three focal traits. Direct and total longitudinal selection plotted for the three traits (±SE): **(A)** flowering time, **(B)** duration, **(C)** total flowers. Points in grey conflict zones indicate opposing significant signs of selection estimates. Even populations are indicated by the blue points, and clumped populations are indicated by yellow and orange points. Dark blue and dark orange points are estimates from the early season run and light blue and yellow points are from the late season run.

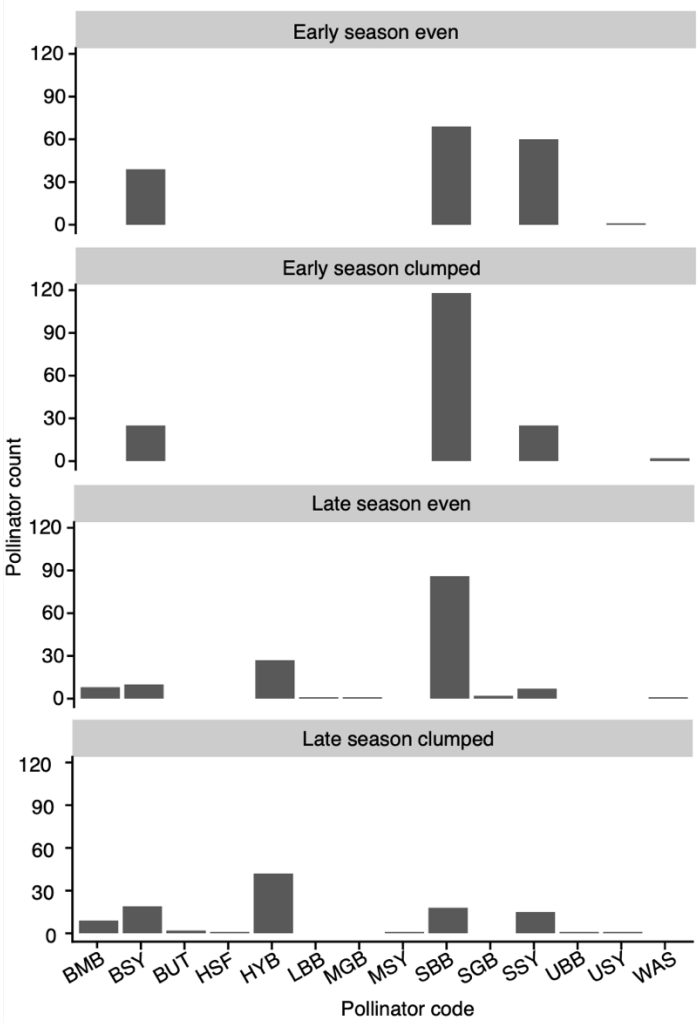

Figure S2. Pollinator counts by pollinator category for each of the four plots (BMB = bumblebee, BSY = big syrphid fly, BUT = butterfly, HSF = house fly, HYB = honey bee, LBB = large black bee, MGB = medium green bee, MSY = medium syrphid fly, SBB = small black bee, SGB = small green bee, SSY = small syrphid fly, UBB = unknown black bee, USY = unknown syrphid fly, WAS = wasp). Pollinator counts were obtained when we conducted six five-minute pollinator observation periods every four to eight days at each of the four plots. Each observation period included a gene-trap plant and the six closest plot plant positions. We recorded all insects that visited a reproductive structure on one of the observed plants. We did not collect the pollinators, so as to not impact the pollinator community.

Supplementary Tables

Table S1. Information about the gene-trap plant batches for early and late season populations. Batches are gene-trap plants that were placed into the experimental plots on the first day of the 'gene-trap time period' and removed on the last day. Approximately twelve offspring were genotyped from each of the six gene-trap plants from each batch.

Gene-trap batch	Gene-trap time period	Gene-trap offspring genotyped (even plot)	Gene-trap offspring genotyped (clumped plot)
Early season (1.1)	4-7 July	72	67
Early season (1.2)	11-14 July	71	39
Early season (1.3)	14-21 July	48	77
Early season (1.4)	21-25 July	55	51
Early season (1.5)	25-28 July	68	49
Early season (1.6)	28-July-1 August	69	60
Early season (1.7)	1-11 August	70	30
Late season (2.1)	16-20 August	72	71
Late season (2.2)	24-28 August	73	71
Late season (2.3)	1-5 September	72	72
Late season (2.4)	9-13 September	70	72
Late season (2.5)	17-21 September	71	72
Late season (2.6)	25-29 September	72	71
Late season (2.7)	3-7 October	71	72
Late season (2.8)	7-13 October	71	71

1222 **Table S2.** Microsatellite primer information.

Locus	F primer sequence	R primer sequence	Repeat motif	Annealing temperature °C	ε1	ε2	Primer source
BRMS-005	ACCTCCTGCAGATTCGTGTC	GCTGACCTTTCTTACCGCTC	$(GA)_{13}$	60	0.052449	0.013805	Suwabe et al., 2002
BRMS-007	AAATTGTTTCTCTTCCCCAT	GTGTTAGGGAGCTGGAGAAT	$(CT)_{24}$	45	0.022207	0.047789	Suwabe et al., 2002
BRMS-019	CCCAAACGCTTTTGACACAT	GGCACAATCCACTCAGCTTT	$(GT)_{10}$	60	0.063575	0.006244	Suwabe et al., 2002
BRMS-033	GCGGAAACGAACACTCCTCCCATGT	CCTCCTTGTGCTTTCCCTGGAGACG	$(CA)_{11}$	60	0.010682	0.006696	Suwabe et al., 2002
BRMS-037	CTGCTCGCATTTTTTATCATAC	TACGCTTGGGAGAGAAAACTAT	$(CA)_{10}$	56	0.024997	0.03898	Suwabe et al., 2002
BRMS-042-2	GGATCAGTTATCTGCACCACAA	TCGGAATTGGATAAGAATTCAA	$(GA)_4(CT)_{26}$	60	0.024431	0.004467	Suwabe et al., 2002
Na10-A08	CATGGTTAAAACAATGGCCC	CAAGAAACACCATCATTTCTCA	$(GA)_{21}$	58	0.013953	0.002916	Lowe et al., 2004

Locus	F primer sequence	R primer sequence	Repeat motif	Annealing temperature °C	ε1	ε2	Primer source
Na10-D09	AAGAACGTCAAGATCCTCTGC	ACCACCACGGTAGTAGAGCG	$(GA)_{24}$	61	0.036447	0.005979	Lowe et al., 2004
Na12-E02	TTGAAGTAGTTGGAGTAATTGGAGG	CAGCAGCCACAACCTTACG	$(TTG)_{13}$	55	0.007782	0.008447	Lowe et al., 2004
Ra2-A05	GCTAGTTTACGCGGCGG	AAACGACATCGGCAAAGAAG	$(GGC)_{6}$	50	0.009597	0.006421	Lowe et al., 2004

Table SX. Microsatellite primer information.

Table S3. Tables providing mean, standard deviation, naive standard error, and batch and plot identifiers for both direct and total selection estimates in longitudinal and cross-sectional analyses for the three phenotypes flowering time, duration of flowering, and total flowers.

Direct selection estimates (flowering time)				
Mean	**SD**	**Naive.SE**	**batch_id**	**Plot**
-0.006981909	0.028531554	0.000902247	Overall	Early season clumped
0.015903295	0.015035075	0.000475451	Overall	Late season clumped
-0.01608615	0.021168351	0.000669402	Overall	Early season even
0.00332643	0.017943455	0.000567422	Overall	Late season even
-0.375596626	0.098439972	0.003112945	1.1	Early season clumped
0.025871576	0.068861019	0.002177577	1.2	Early season clumped
-0.002016799	0.038472298	0.001216601	1.3	Early season clumped
-0.003970546	0.05747295	0.001817454	1.4	Early season clumped
0.000380185	0.047107278	0.001489663	1.5	Early season clumped
0.146935381	0.048386808	0.001530125	1.6	Early season clumped
0.089617636	0.111987284	0.003541349	1.7	Early season clumped
-8.151834252	6.138518812	0.194117009	2.1	Late season clumped
-0.158231295	0.03924648	0.001241083	2.2	Late season clumped
-0.046718881	0.024993799	0.000790373	2.3	Late season clumped
0.048687282	0.026372259	0.000833964	2.4	Late season clumped
0.102996043	0.026697738	0.000844257	2.5	Late season clumped
0.071973383	0.024355838	0.000770199	2.6	Late season clumped
0.17962825	0.039616412	0.001252781	2.7	Late season clumped
0.56566521	0.105095761	0.00332342	2.8	Late season clumped
-0.242616427	0.080214745	0.002536613	1.1	Early season even
-0.199546906	0.047097617	0.001489357	1.2	Early season even
-0.055462348	0.042598907	0.001347096	1.3	Early season even
0.008392488	0.037678651	0.001191504	1.4	Early season even
0.019336944	0.030348842	0.000959715	1.5	Early season even

0.079555724	0.030462853	0.00096332	1.6	Early season even
0.169496117	0.035322689	0.001117001	1.7	Early season even
-16.74500507	6.94164946	0.21951423	2.1	Late season even
-0.206475354	0.036369289	0.001150098	2.2	Late season even
0.014245518	0.026199672	0.000828506	2.3	Late season even
-0.002361999	0.027747698	0.000877459	2.4	Late season even
0.079928258	0.030323221	0.000958904	2.5	Late season even
0.229932993	0.043773556	0.001384241	2.6	Late season even
0.083331634	0.055573654	0.001757393	2.7	Late season even
-0.062178147	0.060055837	0.001899132	2.8	Late season even

Direct selection estimates (duration)				
Mean	**SD**	**Naive.SE**	**batch_id**	**Plot**
0.00882696	0.02500533	0.00079074	Overall	Early season clumped
0.02652461	0.01102161	0.00034853	Overall	Late season clumped
0.01132943	0.018089	0.00057202	Overall	Early season even
0.01154386	0.00985931	0.00031178	Overall	Late season even
-0.2815545	0.07362382	0.00232819	1.1	Early season clumped
0.00762596	0.0587306	0.00185722	1.2	Early season clumped
-0.099965	0.04848925	0.00153336	1.3	Early season clumped
-0.0343674	0.04663158	0.00147462	1.4	Early season clumped
-0.002068	0.04242457	0.00134158	1.5	Early season clumped
0.15472886	0.02680204	0.00084755	1.6	Early season clumped
0.2080262	0.07628213	0.00241225	1.7	Early season clumped
0.0628585	0.08120299	0.00256786	2.1	Late season clumped
0.03028139	0.01491263	0.00047158	2.2	Late season clumped
-0.0223375	0.01999688	0.00063236	2.3	Late season clumped
0.0227997	0.0184814	0.00058443	2.4	Late season clumped
0.04676684	0.01831795	0.00057926	2.5	Late season clumped
0.10846698	0.01892437	0.00059844	2.6	Late season clumped
0.16481722	0.0334763	0.00105861	2.7	Late season clumped
0.48793196	0.11279371	0.00356685	2.8	Late season clumped
0.05026352	0.03764932	0.00119058	1.1	Early season even
-0.0182263	0.03497106	0.00110588	1.2	Early season even
0.02385683	0.03355934	0.00106124	1.3	Early season even
0.00985617	0.03240137	0.00102462	1.4	Early season even
0.04074949	0.03014128	0.00095315	1.5	Early season even
0.09346784	0.02964106	0.00093733	1.6	Early season even
0.1798256	0.03475848	0.00109916	1.7	Early season even

0.04241331	0.01660166	0.00052499	2.1	Late season even
0.0113336	0.01784886	0.00056443	2.2	Late season even
0.00450894	0.01532011	0.00048446	2.3	Late season even
0.01477747	0.01447289	0.00045767	2.4	Late season even
-0.010332	0.01765665	0.00055835	2.5	Late season even
-0.01189	0.02315772	0.00073231	2.6	Late season even
0.01259347	0.02192172	0.00069323	2.7	Late season even
0.03622488	0.02324671	0.00073513	2.8	Late season even

Direct selection estimates (total flowers)				
Mean	**SD**	**Naive.SE**	**batch_id**	**Plot**
0.00510838	0.00605554	0.00019149	Overall	Early season clumped
0.00523285	0.00331455	0.00010482	Overall	Late season clumped
0.00680454	0.00286065	9.05E-05	Overall	Early season even
0.01631161	0.00294164	9.30E-05	Overall	Late season even
-0.0309894	0.01658643	0.00052451	1.1	Early season clumped
-0.0123147	0.01359962	0.00043006	1.2	Early season clumped
0.00475529	0.00986638	0.000312	1.3	Early season clumped
0.03381944	0.00944064	0.00029854	1.4	Early season clumped
0.01759863	0.00893975	0.0002827	1.5	Early season clumped
0.00182576	0.00931115	0.00029444	1.6	Early season clumped
0.02604876	0.01752567	0.00055421	1.7	Early season clumped
0.00953891	0.00984681	0.00031138	2.1	Late season clumped
0.00477074	0.00490168	0.00015501	2.2	Late season clumped
0.0094166	0.00581673	0.00018394	2.3	Late season clumped
0.00568217	0.00592814	0.00018746	2.4	Late season clumped
0.02042128	0.00482642	0.00015263	2.5	Late season clumped
0.01194299	0.00501812	0.00015869	2.6	Late season clumped
-0.0009671	0.00562092	0.00017775	2.7	Late season clumped
0.01230085	0.0047433	0.00015	2.8	Late season clumped
-0.0013418	0.0061301	0.00019385	1.1	Early season even
-0.003449	0.00570091	0.00018028	1.2	Early season even
0.00547881	0.0058345	0.0001845	1.3	Early season even
0.01221124	0.00466883	0.00014764	1.4	Early season even
0.01302366	0.00354156	0.00011199	1.5	Early season even
0.01435457	0.00303726	9.60E-05	1.6	Early season even
0.00379067	0.00459429	0.00014528	1.7	Early season even

0.01485659	0.01048946	0.00033171	2.1	Late season even
0.01799558	0.00803002	0.00025393	2.2	Late season even
-0.0004183	0.00578559	0.00018296	2.3	Late season even
0.01462476	0.00516053	0.00016319	2.4	Late season even
0.01467727	0.00472552	0.00014943	2.5	Late season even
0.01156951	0.00505552	0.00015987	2.6	Late season even
0.01390219	0.0041293	0.00013058	2.7	Late season even
0.02279289	0.00347257	0.00010981	2.8	Late season even

Total selection estimates (indirect + direct) (flowering time)				
Mean	**SD**	**Naive.SE**	**batch_id**	**Plot**
-0.006245153	0.027145249	0.000858408	Overall	Early season clumped
0.000502176	0.015385134	0.000486521	Overall	Late season clumped
-0.017027673	0.021456522	0.000678515	Overall	Early season even
0.000755943	0.017899217	0.000566023	Overall	Late season even
-0.116477424	0.075047471	0.002373209	1.1	Early season clumped
0.061961986	0.063664127	0.002013236	1.2	Early season clumped
0.016895209	0.037927546	0.001199374	1.3	Early season clumped
0.047557717	0.050022058	0.001581836	1.4	Early season clumped
-0.006949878	0.037874006	0.001197681	1.5	Early season clumped
0.052937902	0.035993165	0.001138204	1.6	Early season clumped
-0.118205263	0.060980513	0.001928373	1.7	Early season clumped
-1.206140182	0.316204997	0.00999928	2.1	Late season clumped
-0.13720504	0.036369516	0.001150105	2.2	Late season clumped
-0.056717202	0.024387774	0.000771209	2.3	Late season clumped
0.027278464	0.024642487	0.000779264	2.4	Late season clumped
0.079986311	0.029759593	0.000941081	2.5	Late season clumped
-0.006080636	0.02331375	0.000737246	2.6	Late season clumped
0.046692645	0.02598787	0.000821809	2.7	Late season clumped
0.212382724	0.049964516	0.001580017	2.8	Late season clumped
-0.237546966	0.080386225	0.002542036	1.1	Early season even
-0.136520557	0.046521306	0.001471133	1.2	Early season even
-0.041817789	0.044178334	0.001397042	1.3	Early season even
0.017976659	0.039324229	0.001243541	1.4	Early season even
-0.00075705	0.029611497	0.000936398	1.5	Early season even
0.030183431	0.026266082	0.000830606	1.6	Early season even
0.027862096	0.01488759	0.000470787	1.7	Early season even

-8.387812769	5.225045121	0.165230435	2.1	Late season even
-0.178649154	0.034457995	0.001089657	2.2	Late season even
0.019579195	0.026755947	0.000846097	2.3	Late season even
-0.004850016	0.026920949	0.000851315	2.4	Late season even
0.076617595	0.030610104	0.000967976	2.5	Late season even
0.231011633	0.043631702	0.001379756	2.6	Late season even
0.074558702	0.041999864	0.001328152	2.7	Late season even
-0.073420909	0.040465859	0.001279643	2.8	Late season even

Total selection estimates (indirect + direct) (duration)				
Mean	**SD**	**Naive.SE**	**batch_id**	**Plot**
0.00888715	0.02414921	0.00076366	Overall	Early season clumped
0.03611464	0.00922804	0.00029182	Overall	Late season clumped
0.02701842	0.01631411	0.0005159	Overall	Early season even
0.0075893	0.00924095	0.00029222	Overall	Late season even
-0.1645653	0.05422724	0.00171482	1.1	Early season clumped
-0.0682685	0.06698963	0.0021184	1.2	Early season clumped
-0.1030512	0.04537273	0.00143481	1.3	Early season clumped
-0.0204566	0.04660923	0.00147391	1.4	Early season clumped
0.01016517	0.03782852	0.00119624	1.5	Early season clumped
0.12356042	0.02360052	0.00074631	1.6	Early season clumped
0.15860709	0.03610699	0.0011418	1.7	Early season clumped
-0.1768025	0.04110923	0.00129999	2.1	Late season clumped
0.04090976	0.01280845	0.00040504	2.2	Late season clumped
-0.0119696	0.01729475	0.00054691	2.3	Late season clumped
0.0342684	0.01641246	0.00051901	2.4	Late season clumped
0.08307472	0.01483972	0.00046927	2.5	Late season clumped
0.09911	0.01459202	0.00046144	2.6	Late season clumped
0.05598788	0.01618212	0.00051172	2.7	Late season clumped
0.01832311	0.0185168	0.00058555	2.8	Late season clumped
0.03103956	0.03212403	0.00101585	1.1	Early season even
-0.0243458	0.03432544	0.00108547	1.2	Early season even
0.02939477	0.03282804	0.00103811	1.3	Early season even
0.01956398	0.03261906	0.00103151	1.4	Early season even
0.04881801	0.02628494	0.0008312	1.5	Early season even
0.05201642	0.02455114	0.00077638	1.6	Early season even
0.05122485	0.02216105	0.00070079	1.7	Early season even

-0.0228835	0.01942158	0.00061416	2.1	Late season even
0.02265316	0.0178791	0.00056539	2.2	Late season even
0.00307507	0.01677021	0.00053032	2.3	Late season even
0.01056311	0.0145205	0.00045918	2.4	Late season even
-0.013963	0.01668804	0.00052772	2.5	Late season even
-0.0367376	0.02208735	0.00069846	2.6	Late season even
-0.0291383	0.0208311	0.00065874	2.7	Late season even
-0.0041043	0.02183622	0.00069052	2.8	Late season even

Total selection estimates (indirect + direct) (total flowers)				
Mean	**SD**	**Naive.SE**	**batch_id**	**Plot**
0.00591626	0.00594727	0.00018807	Overall	Early season clumped
0.00901461	0.00274265	8.67E-05	Overall	Late season clumped
0.00535489	0.00261246	8.26E-05	Overall	Early season even
0.01442986	0.00286848	9.07E-05	Overall	Late season even
-0.0257099	0.01352754	0.00042778	1.1	Early season clumped
-0.0135148	0.01398149	0.00044213	1.2	Early season clumped
-0.0050195	0.00973243	0.00030777	1.3	Early season clumped
0.02894547	0.00901032	0.00028493	1.4	Early season clumped
0.01443122	0.00875107	0.00027673	1.5	Early season clumped
0.00321208	0.00784956	0.00024823	1.6	Early season clumped
0.01296748	0.00929735	0.00029401	1.7	Early season clumped
-0.0300788	0.00686928	0.00021723	2.1	Late season clumped
0.01255315	0.00444451	0.00014055	2.2	Late season clumped
0.00624272	0.00506644	0.00016022	2.3	Late season clumped
0.00758897	0.0045251	0.0001431	2.4	Late season clumped
0.01863653	0.00397083	0.00012557	2.5	Late season clumped
0.01657257	0.00410618	0.00012985	2.6	Late season clumped
0.00404817	0.00493065	0.00015592	2.7	Late season clumped
0.00401624	0.0047312	0.00014961	2.8	Late season clumped
0.00478586	0.00600942	0.00019004	1.1	Early season even
-0.0038417	0.00619016	0.00019575	1.2	Early season even
0.00336287	0.00575715	0.00018206	1.3	Early season even
0.00909441	0.00458465	0.00014498	1.4	Early season even
0.01144983	0.00339332	0.00010731	1.5	Early season even
0.01060982	0.00290363	9.18E-05	1.6	Early season even
-0.0072674	0.00398486	0.00012601	1.7	Early season even

-0.0229094	0.00861401	0.0002724	2.1	Late season even
0.00479196	0.006677	0.00021115	2.2	Late season even
-0.0001432	0.00580432	0.00018355	2.3	Late season even
0.01322361	0.00520336	0.00016455	2.4	Late season even
0.01482225	0.00488533	0.00015449	2.5	Late season even
0.00748422	0.00538035	0.00017014	2.6	Late season even
0.01119549	0.00374181	0.00011833	2.7	Late season even
0.02101552	0.00337827	0.00010683	2.8	Late season even

Table S4. Distance decay coefficients overall and by cross-section, standard deviation (SD), naive standard error (Naive.SE), batch unique identifier, and plot identification.

Mean	SD	Naive.SE	Time.series.SE	batch_id	Plot
-0.317837465	0.044689822	0.001413216	0.001413216	Overall	Early season clumped
-0.510805082	0.074624019	0.002359819	0.002359819	1.1	Early season clumped
-0.322985353	0.101972742	0.003224661	0.003224661	1.2	Early season clumped
-0.268203257	0.066243369	0.002094799	0.002094799	1.3	Early season clumped
-0.507300335	0.108578235	0.003433545	0.003590788	1.4	Early season clumped
-0.263970904	0.06997566	0.002212825	0.002212825	1.5	Early season clumped
-0.096257626	0.074744094	0.002363616	0.002317706	1.6	Early season clumped
-0.427581789	0.116611641	0.003687584	0.003687584	1.7	Early season clumped

Mean	SD	Naive.SE	Time.series.SE	batch_id	Plot
-0.341095528	0.036489575	0.001153902	0.001210716	Overall	Late season clumped
-0.308492813	0.066002057	0.002087168	0.002087168	2.1	Late season clumped
-0.392679726	0.070532759	0.002230442	0.002230442	2.2	Late season clumped
-0.636592274	0.09309287	0.002943855	0.002943855	2.3	Late season clumped
-0.454286413	0.07547378	0.00238669	0.002252077	2.4	Late season clumped
-0.327838819	0.061945003	0.001958873	0.001958873	2.5	Late season clumped
-0.351887491	0.057437166	0.001816323	0.001816323	2.6	Late season clumped
-0.373146439	0.063896589	0.002020588	0.002020588	2.7	Late season clumped
-0.436147964	0.067142277	0.002123225	0.002268596	2.8	Late season clumped

Mean	SD	Naive.SE	Time.series.SE	batch_id	Plot
-0.797697697	0.085003163	0.002688036	0.002688036	Overall	Early season even
-0.552820264	0.13505356	0.004270769	0.004270769	1.1	Early season even
-1.744651908	0.232391077	0.007348851	0.008646116	1.2	Early season even
-1.161193606	0.247805254	0.00783629	0.00783629	1.3	Early season even

-0.98966918	0.169600111	0.005363226	0.005363226	1.4	Early season even
-0.547981383	0.120386754	0.003806963	0.003461145	1.5	Early season even
-0.52810649	0.11458752	0.003623576	0.003623576	1.6	Early season even
-0.509307717	0.120664344	0.003815742	0.003815742	1.7	Early season even
Mean	**SD**	**Naive.SE**	**Time.series.SE**	**batch_id**	**Plot**
-0.618860274	0.071623246	0.002264926	0.002264926	Overall	Late season even
-0.413540403	0.099965021	0.003161172	0.003161172	2.1	Late season even
-0.357433907	0.118675583	0.003752851	0.003752851	2.2	Late season even
-1.103726098	0.181458818	0.005738232	0.005738232	2.3	Late season even
-0.638494874	0.116795807	0.003693408	0.003877345	2.4	Late season even
-0.391249216	0.114403781	0.003617765	0.003414186	2.5	Late season even
-0.607766055	0.121406375	0.003839207	0.003839207	2.6	Late season even
-0.453230443	0.115335253	0.003647221	0.003617791	2.7	Late season even
-0.23110786	0.119146619	0.003767747	0.003767747	2.8	Late season even

Table S5. Pearson correlation coefficients for all variables overall and by cross-section, p-value, batch id indicating the interval, and the population type. .

variable 1	variable 2	correlation coefficient (r)	p-value	batch_id	population
flowering time	duration	-0.108796	0.1168646	overall	early season even
flowering time	total flowers	-0.1694515	0.01417473	overall	early season even
duration	total flowers	0.30625275	6.49E-06	overall	early season even
flowering time	duration	-0.122673	0.07197802	overall	early season clumped
flowering time	total flowers	-0.0005354	0.99375777	overall	early season clumped
duration	total flowers	0.32026702	1.53E-06	overall	early season clumped
flowering time	duration	0.05469244	0.42933741	overall	late season even
flowering time	total flowers	0.24278174	0.00037219	overall	late season even
duration	total flowers	-0.0032296	0.96280442	overall	late season even
flowering time	duration	0.2238422	0.00092353	overall	late season clumped
flowering time	total flowers	-0.0882211	0.19650397	overall	late season clumped
duration	total flowers	0.52273278	0	overall	late season clumped
flowering time	duration	0.03124778	0.73914524	1.1	early season even
flowering time	total flowers	-0.1059658	0.25758493	1.1	early season even
duration	total flowers	0.16656088	0.07393866	1.1	early season even
flowering time	duration	0.02166525	0.7691269	1.2	early season even
flowering time	total flowers	-0.1097976	0.13573603	1.2	early season even
duration	total flowers	0.25179106	0.0005266	1.2	early season even
flowering time	duration	-0.0036244	9.59E-01	1.3	early season even
flowering time	total flowers	-0.0903504	0.19873559	1.3	early season even
duration	total flowers	0.28134582	4.57E-05	1.3	early season even
flowering time	duration	-0.087612	0.29811014	1.4	early season even
flowering time	total flowers	0.00420594	9.60E-01	1.4	early season even
duration	total flowers	0.20330619	0.01487775	1.4	early season even
flowering time	duration	-0.3014413	0.0029919	1.5	early season even
flowering time	total flowers	-0.1012531	0.32889555	1.5	early season even
duration	total flowers	0.14085603	0.17334982	1.5	early season even
flowering time	duration	-0.4644519	0.00024002	1.6	early season even

flowering time	total flowers	-0.0818464	0.54134498	1.6	early season even
duration	total flowers	0.03724077	0.78136586	1.6	early season even
flowering time	duration	-0.758817	8.19E-08	1.7	early season even
flowering time	total flowers	-0.2486999	0.14356848	1.7	early season even
duration	total flowers	0.08920431	0.60489775	1.7	early season even
flowering time	duration	-0.1789834	0.04407399	1.1	early season clumped
flowering time	total flowers	-0.1261353	0.15763571	1.1	early season clumped
duration	total flowers	0.33315217	0.00012959	1.1	early season clumped
flowering time	duration	-0.1899769	0.00586691	1.2	early season clumped
flowering time	total flowers	0.03126849	0.65311268	1.2	early season clumped
duration	total flowers	0.35542285	1.29E-07	1.2	early season clumped
flowering time	duration	-0.122673	0.07197802	1.3	early season clumped
flowering time	total flowers	-0.0005354	0.99375777	1.3	early season clumped
duration	total flowers	0.32026702	1.53E-06	1.3	early season clumped
flowering time	duration	-0.3259546	7.54E-05	1.4	early season clumped
flowering time	total flowers	-0.0281776	0.73923031	1.4	early season clumped
duration	total flowers	0.19870562	0.01775868	1.4	early season clumped
flowering time	duration	-0.4302741	0.00130086	1.5	early season clumped
flowering time	total flowers	-0.0836393	0.55155679	1.5	early season clumped
duration	total flowers	0.03612217	0.7973436	1.5	early season clumped
flowering time	duration	-0.2583463	0.13401365	1.6	early season clumped
flowering time	total flowers	-0.1303629	0.45541263	1.6	early season clumped
duration	total flowers	0.28688426	0.09473694	1.6	early season clumped
flowering time	duration	-0.4060562	0.06778209	1.7	early season clumped
flowering time	total flowers	-0.239039	0.2966868	1.7	early season clumped
duration	total flowers	0.30017967	0.18613492	1.7	early season clumped
flowering time	duration	0.386939	0.01135958	2.1	late season clumped
flowering time	total flowers	0.42047224	0.00556198	2.1	late season clumped
duration	total flowers	0.52932245	0.00031292	2.1	late season clumped
flowering time	duration	0.03237528	0.71248374	2.2	late season clumped
flowering time	total flowers	-0.0977349	0.26490164	2.2	late season clumped

duration	total flowers	0.6087358	9.77E-15	2.2	late season clumped
flowering time	duration	0.13939391	0.04957618	2.3	late season clumped
flowering time	total flowers	-0.0824127	0.24718247	2.3	late season clumped
duration	total flowers	0.53765172	2.22E-16	2.3	late season clumped
flowering time	duration	0.03546327	0.65011499	2.4	late season clumped
flowering time	total flowers	-0.3046599	6.58E-05	2.4	late season clumped
duration	total flowers	0.45083624	1.09E-09	2.4	late season clumped
flowering time	duration	-0.0519579	0.54355023	2.5	late season clumped
flowering time	total flowers	-0.3754992	5.24E-06	2.5	late season clumped
duration	total flowers	0.38947149	2.15E-06	2.5	late season clumped
flowering time	duration	-0.2656026	0.0134502	2.6	late season clumped
flowering time	total flowers	-0.3492361	0.00098172	2.6	late season clumped
duration	total flowers	0.39767881	0.00014969	2.6	late season clumped
flowering time	duration	-0.4220204	0.0092751	2.7	late season clumped
flowering time	total flowers	-0.2963079	0.07495489	2.7	late season clumped
duration	total flowers	0.43483869	0.00715556	2.7	late season clumped
flowering time	duration	-0.4763618	0.01038847	2.8	late season clumped
flowering time	total flowers	-0.3063095	0.11289407	2.8	late season clumped
duration	total flowers	0.43593564	0.02039783	2.8	late season clumped
flowering time	duration	0.16585614	0.30003689	2.1	late season even
flowering time	total flowers	0.29738475	0.05898921	2.1	late season even
duration	total flowers	0.21022224	0.1870857	2.1	late season even
flowering time	duration	0.01634887	0.85409787	2.2	late season even
flowering time	total flowers	0.2036342	0.02063286	2.2	late season even
duration	total flowers	0.06001309	0.49929938	2.2	late season even
flowering time	duration	0.0886604	0.22382051	2.3	late season even
flowering time	total flowers	0.23537003	0.00107931	2.3	late season even
duration	total flowers	0.01783815	0.80701488	2.3	late season even
flowering time	duration	0.02431246	0.76775072	2.4	late season even
flowering time	total flowers	0.05644605	0.49265999	2.4	late season even
duration	total flowers	-0.0307412	0.70882124	2.4	late season even

flowering time	duration	0.001234	0.98892637	2.5	late season even
flowering time	total flowers	-0.0085442	0.92344068	2.5	late season even
duration	total flowers	-0.0445466	0.61617654	2.5	late season even
flowering time	duration	0.09496412	0.37057185	2.6	late season even
flowering time	total flowers	-0.0242579	0.81945937	2.6	late season even
duration	total flowers	-0.0453514	0.6694783	2.6	late season even
flowering time	duration	-0.0632892	0.70979335	2.7	late season even
flowering time	total flowers	0.14199825	0.40183076	2.7	late season even
duration	total flowers	-0.1818482	0.28139682	2.7	late season even
flowering time	duration	0.04286	0.81892107	2.8	late season even
flowering time	total flowers	-0.0679444	0.71647574	2.8	late season even
duration	total flowers	-0.3198476	0.07941965	2.8	late season even