Viewpoints

Explaining the apparent paradox of persistent selection for early flowering

Summary

Decades of observation in natural plant populations have revealed pervasive phenotypic selection for early flowering onset. This consistent pattern seems at odds with life-history theory, which predicts stabilizing selection on age and size at reproduction. Why is selection for later flowering rare? Moreover, extensive evidence demonstrates that flowering time can and does evolve. What maintains ongoing directional selection for early flowering? Several non-mutually exclusive processes can help to reconcile the apparent paradox of selection for early flowering. We outline four: selection through other fitness components may counter observed fecundity selection for early flowering; asymmetry in the flowering-time–fitness function may make selection for later flowering hard to detect; flowering time and fitness may be condition-dependent; and selection on flowering duration is largely unaccounted for. In this Viewpoint, we develop these four mechanisms, and highlight areas where further study will improve our understanding of flowering-time evolution.

Introduction

Flowering at the correct time is critical to plant fitness. Timing of flowering onset determines the environmental conditions experienced during pollen, ovule, and seed development (Rathcke & Lacey, 1985), and the nature of interactions with mutualists (e.g. pollinators, O'Connell & Johnston, 1998; Thomson, 2010; Rafferty & Ives, 2011) and antagonists (e.g. seed predators, Augspurger, 1981; Pilson, 2000; Parachnowitsch & Caruso, 2008). Because flowering amounts to committing meristems to reproduction rather than to vegetative growth, flowering time affects plant size, growth patterns, and architecture (Geber, 1990; Duffy *et al.*, 1999; Kudoh *et al.*, 2002). Within a community context, co-flowering with other species may intensify competition for (or facilitate access to) pollinators or abiotic resources (Mosquin, 1971; Stiles, 1977; Waser, 1978; Kunin, 1993). For these and other reasons, we expect natural selection to direct population mean flowering time towards a local optimum. There is, however, no a priori expectation that selection should act predominantly in one direction. Yet several meta-analyses and reviews (Geber & Griffen, 2003; Harder & Johnson, 2009; Munguía-Rosas *et al.*, 2011) have demonstrated not only that phenotypic selection acts on flowering time, but also that *early* flowering is overwhelmingly favoured. Why?

A rich body of life-history theory establishes testable predictions for the evolution of flowering time (e.g. Cohen, 1971; King & Roughgarden, 1983; Ejsmond *et al.*, 2010; for overviews see Stearns, 1976; Roff, 1993). Almost all life-history models assume a trade-off between the timing-of and size-at reproduction, such that plants that flower early flower at a small size. The optimal timing of reproduction depends on the rate of pre-reproduction mortality and on season length (e.g. as dictated by a killing frost or drought onset). High mortality rates and/or short seasons favour flowering earlier, at a smaller size, and thus, with fewer resources; low mortality rates and longer seasons favour later flowering. Selection arises from the size–time trade-off. Plants switching from growth to reproduction too early will mature seed before the end of the growing season, but are small with fewer resources to invest in reproduction. Those making the switch late are large and have ample resources to support reproduction, but risk mortality before seed maturation. If a population is at its flowering-time optimum, selection is expected to be stabilizing or weak. It is only when early-life mortality rate or season length changes (e.g. through global change, dispersal to a new environment, range expansion, etc.) that directional selection should act to shift the population mean.

Exhaustive empirical evidence supports the basic premise that flowering time evolves through natural selection. Several species exhibit geographic clines in flowering time corresponding to season-length clines (e.g. Van Dijk *et al.*, 1997; Stinchcombe *et al.*, 2004; Wadgymar *et al.*, 2015), and reciprocal-transplant experiments frequently reveal these to be adaptive (e.g. Griffith & Watson, 2005; Hall & Willis, 2006; Colautti & Barrett, 2010; Ågren & Schemske, 2012; Anderson & Gezon, 2015). Moreover, evolutionary responses to selection on flowering time have been observed during artificial selection (e.g. Dorn & Mitchell-Olds, 1991; Burgess *et al.*, 2007; Van Dijk, 2009; Sheth & Angert, 2016), local environmental change (Franks *et al.*, 2007), and species invasion (Montague *et al.*, 2007; Hodgins & Rieseberg, 2011; Turner *et al.*, 2014). Herein lies a paradox. (1) If selection truly favours early flowering most of the time, and plants can respond to that selection, why does selection for earliness persist? (2) Why is phenotypic selection for later flowering rare?

Ongoing global change may be partially responsible for widespread selection for early flowering (Anderson *et al.*, 2012). Advancing flowering phenology has been well documented globally (Fitter & Fitter, 2002; Amano *et al.*, 2010; Ellwood *et al.*, 2013), and some of the advances (particularly in short-lived species) could represent evolutionary responses to shortened seasons or increased juvenile mortality (e.g. Franks *et al.*, 2007; Anderson *et al.*, 2012). However, season length is not universally decreasing – in fact, global change is often associated with lengthening seasons (Kunkel *et al.*, 2004; Reyes-Fox *et al.*, 2014) – and the observed changes in flowering phenology of perennials are likely predominantly plastic. Moreover, selection often favours early flowering even in growth chamber, glasshouse, and garden environments with negligible mortality (e.g. Simonsen & Stinchcombe, 2010; Kenney *et al.*, 2014; Stock *et al.*, 2015). The prevalence of phenotypic selection for early flowering therefore demands other explanations.

In this Viewpoint, we examine four non-mutually exclusive mechanisms that could produce (apparent) selection for early flowering. Where appropriate, we draw attention to parallels in the animal literature. Previous reviews (Rathcke & Lacey, 1985; Primack, 1987; Elzinga *et al.*, 2007; Ehrlén, 2015) helped to motivate the studies that have revealed the pattern of selection for early flowering. Now that the pattern has been documented, we aim to motivate studies that will explain it.

Selection through other fitness components may balance fecundity selection

The widespread pattern of phenotypic selection favouring early flowering generally rests on observations of just one fitness component: fecundity (i.e. the association between flowering time and seed production). The focus on fecundity selection neglects the expectation of multiple episodes of selection on flowering time throughout the life-cycle (Primack, 1987; Ehrlén, 2015). For example, where flowering time is genetically correlated with herbivore resistance (Weinig *et al.*, 2003; Colautti *et al.*, 2017), water-use efficiency (McKay *et al.*, 2003; Kenney *et al.*, 2014), functional traits associated with resource acquisition (Sheth & Angert, 2016), or other traits, flowering-time genotype likely predicts survival to flowering. Selection for late flowering might therefore be occurring early in the life-cycle. Viability selection for late flowering could in principle oppose fecundity selection for early flowering (see Wadgymar *et al.* (2017) for an example), such that total (viability + fecundity) directional selection is weak or absent. Total selection could, in fact, even be stabilizing (McGlothlin, 2010), as is predicted by life-history theory.

Given its potential to account for the paradox of persistent selection for early flowering without response, estimating early-acting viability selection on flowering time is a research priority. Of course, estimating the effect of a trait on survival before that trait is expressed (i.e. selection on the 'invisible fraction', Grafen, 1988) is inherently difficult (Hadfield, 2008). Solutions include recording mortality in pedigreed populations (e.g. Mojica & Kelly, 2010; see also Sinervo & McAdam (2008) for example in side-blotched lizards), and experimental manipulations that 'rescue' the invisible fraction from early mortality. Bennington & McGraw (1995), for example, thinned either small plants likely to die before flowering (conventional thinning), or large plants that would have otherwise crowded small individuals (invisible fraction rescue) to observe effects on adult trait distribution and selection in experimental populations of jewelweed (*Impatiens pallida*). An additional strategy could be to apply artificial viability selection to an early-life trait (e.g. water-use efficiency), and measure any correlated response in flowering time over generations. This approach awaits testing.

Asymmetry in the fitness function makes selection for late flowering harder to detect

Under certain conditions, the function relating the timing of a life-history event to fitness is expected to be asymmetric (e.g. Fig. 2a in King & Roughgarden, 1983), a point recognized in animals (Mountford, 1968; Singer & Parmesan, 2010). Asymmetry in the fitness function arises because the penalty for reproducing too late (reproductive failure) is stronger than that for reproducing too early (fewer resources to invest in offspring production). As a result, populations flowering earlier than the local optimum experience weaker selection than populations flowering later than the optimum (Fig. 1; Fig. 1b in Weis *et al.*, 2014), and weaker selection differentials are harder to detect. In fact, population mean flowering time could be oscillating around its local optimum, but we would fail to recognize the net neutral nature of selection over seasons/generations because we only detect selection when the mean falls on the late side of the optimum.

Populations generally do not occupy the entire hypothetical range of phenotypic space (Wright, 1932; Kingsolver, 1988). Ascertaining the shape of the full fitness function therefore requires artificially enhancing phenotypic variance in flowering time, for example by manipulating flowering times (Shitaka & Hirose, 1998), sampling (or crossing) individuals from populations with divergent flowering times (Weis *et al.*, 2014), or mathematically constructing absent phenotypes (O'Neil, 1999). Furthermore, detecting asymmetry in the fitness function requires statistical tools beyond the linear and quadratic regression typically employed in selection analysis. Weis *et al.* (2014) demonstrate the application of useful methods including locally weighted polynomial regression, parametric nonlinear regression, and piecewise regression; other options include cubic splines (Schluter & Nychka, 1994) and their generalizations (Morrissey & Sakrejda, 2013).

Flowering time, size, and fitness are condition-dependent

The predictions of life-history theory rest on a trade-off between timing of reproduction and size at reproduction. In natural populations of both annuals and perennials, however, individuals flowering early are often larger than those flowering late; indeed, in 24 of 28 studies surveyed by Forrest (2014), the observed correlation conflicts with the assumed pattern. Larger size with earlier flowering can be explained by condition-dependence: individuals in better condition – whether because of microhabitat quality, age, or stored resources – are able to flower earlier, and at a larger size. Similar arguments are made for birds (Price *et al.*, 1988; Rowe *et al.*, 1994), small mammals (Réale *et al.*, 2003), and insects (Rowe & Ludwig, 1991). Condition-dependence may reflect environmental heterogeneity if individuals with better access to resources grow and flower faster (Ehrlén & Münzbergová, 2009; Forrest, 2014). Consequently, estimates of direct selection on flowering time will be biased by exclusion of an important trait (i.e.

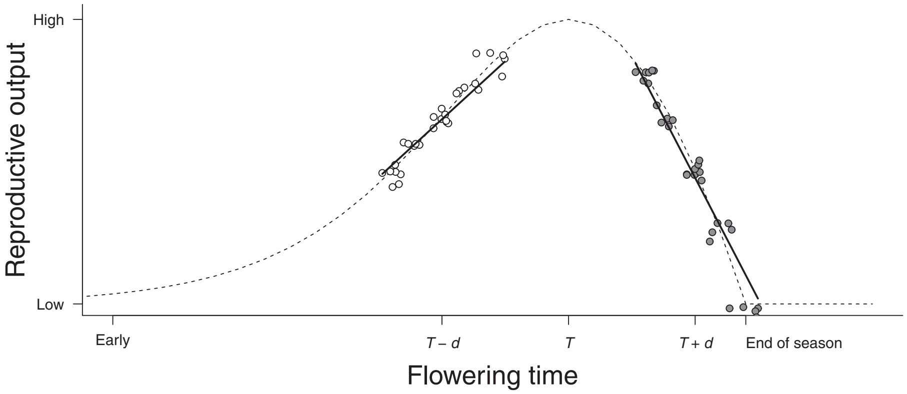

Fig. 1 Conceptual model illustrating the effects of fitness function asymmetry on the strength of selection for early vs late flowering time. Asymmetry arises in the fitness function relating flowering time to reproductive output (dashed line) because the penalty for flowering after the end of the season (reproductive failure) is greater than the penalty for flowering before the optimum (fewer resources to invest in offspring). The exact functional form could differ from that depicted here without affecting conclusions, provided it is asymmetric. Given asymmetry, a population flowering later than the optimum (T), such that mean flowering time = $T + d$ (closed symbols), experiences greater variance in reproductive output, and thus stronger selection, than does an early population with mean flowering time = $T - d$ (open symbols), despite equal variance in flowering time. These may be two distinct populations, or a single population flowering in two different years. Solid lines depict the linear association between flowering time and reproductive output within a population; the slope is steeper for the late-flowering population, particularly when expressed on a scale of relative fitness and standardized flowering time in the calculation of selection differentials. Based on Fig. 1(b) of Weis *et al.* (2014).

condition, or environmental quality) from the analysis (Mitchell-Olds & Shaw, 1987; Rausher, 1992). These biases can be large (Stinchcombe *et al.*, 2002), such that the true nature of direct selection on flowering-time genotypes might differ substantially from the persistent selection for early flowering emerging from meta-analyses of phenotypic selection.

Condition-dependence can also explain the lack of response to pervasive selection for early flowering. If the covariance between flowering time, size, and fitness is purely environmental, then there is no genetic covariance between flowering time and fitness, and response is not possible (Crow & Nagylaki, 1976; Price *et al.*, 1988; Stearns, 1989; Rausher, 1992; Stinchcombe *et al.*, 2002). Three techniques – experimentally dissociating genetically determined flowering times and seasonal conditions (Austen & Weis, 2015), directly manipulating food/nutrient availability (and, thus, condition) across genotypes (e.g. Johansson *et al.*, 2001), and performing genetically based analyses of selection (Rausher, 1992; e.g. Anderson *et al.*, 2011) – can help predict evolutionary responses in the face of environmentally based condition-dependence. Consistent with life-history predictions, at least one genetically based study of selection on flowering time has detected selection for late flowering in a low-mortality environment, and for early flowering in high-mortality environments (Fournier-Level *et al.*, 2013). Others, however, have found selection for early flowering even when mortality rates are low (e.g. Simonsen & Stinchcombe, 2010), suggesting that while condition-dependence may frequently contribute to phenotypic relationships between size, flowering time, and fitness, it is not a complete or universal explanation for pervasive selection for early flowering.

Condition-dependence in the context of selection analysis is often thought of as environmental in nature, but it may also reflect variance in mutation load, because life-history traits like flowering time are likely affected by many loci (Rowe & Houle, 1996). Genetic condition-dependence is particularly likely under the mixed-mating common in flowering plants (Goodwillie *et al.*, 2005): under mixed-mating, individuals vary in their inbreeding coefficient and, thus, their expression of inbreeding depression (Willis, 1996). If the correlation between flowering time and condition is purely genetic, mutation–selection balance will maintain variance in flowering time despite selection (Houle *et al.*, 1996), as the segregating variation affecting flowering time is mainly deleterious. Assuming the expression of deleterious mutations tends to delay flowering, genetically-based condition-dependence also explains the pervasive pattern of selection for earlier flowering: selection always favours increased condition and fitness. Willis (1996) demonstrated that partial inbreeding depression in *Mimulus guttatus* – where some individuals exhibit inbreeding depression for the traits of interest and fitness, while others do not – could significantly bias estimates of phenotypic selection. He reported estimates of phenotypic selection being biased for some traits, including flowering time, by 20–50%. Artificial selection experiments to increase and decrease flowering time would be a helpful test of genetically-based condition-dependence. If genetic variation for flowering time is at mutation–selection balance, then response to selection for late flowering should be accompanied by deleterious pleiotropic effects on other fitness and vigour components, for example growth, size, male fertility, and survivorship. A combined approach to evaluating the environmental and genetic basis of condition-dependence in flowering time is probably required, because both environmental and genetic factors likely underlie condition-dependence in natural populations (Bonduriansky *et al.*, 2015).

Selection is favouring longer flowering duration

Individuals that flower early often flower longer than those that flower late (Hendry & Day, 2005). Their longer flowering duration may be supported by ongoing resource acquisition during reproduction, achieved, for example, by continued addition of vegetative modules during reproduction (e.g. *Chamaecrista* *fasciculata*, *Ipomoea hederacea*, *Medicago lupulina*), or by photosynthetic reproductive organs (Bazzaz & Carlson, 1979; Earley *et al.*, 2009). Ongoing resource acquisition could lessen the penalty for flowering early, by reducing the trade-off between onset and size/resource status (see also point (2) earlier).

Given the correlation between flowering time and duration, we need data on how selection acts on flowering duration to interpret phenotypic selection on flowering time, but this is rarely reported. Just as more days displaying on the lek increases mating opportunity in some animals, a longer flowering duration may increase mating opportunity in plants (Andersson, 1994; Murphy, 1998; Delph & Ashman, 2006), leading to (indirect) selection for early flowering. The strong multicollinearity between flowering time and duration may preclude estimation of selection gradients (which measure direct selection, accounting for correlated traits) on these traits, but alternatives exist. Reporting selection differentials (which measure direct and indirect selection through correlated traits) acting on flowering time and duration (and possibly flower number or display size, e.g. Sandring & Ågren, 2009), along with the correlation between them, is a simple first step (e.g. O'Neil, 1997). Path analysis treating flowering duration as a multiplicative fitness component (Conner, 1996; Austen & Weis, 2016a) offers another approach to isolating fitness effects of flowering time independent of its correlation with duration. Clever experimental designs that allow for variation in flowering time but not duration, and vice versa, might be useful here, although challenging to implement.

Looking forward

Now that we have a documented pattern of phenotypic selection for early flowering, it is time to ascribe mechanisms to the pattern. The four we have described – (1) selection on the invisible fraction, (2) asymmetric fitness functions, (3) condition-dependence, and (4) correlations between flowering onset and duration – can act alone or together to overwhelm the selection for late flowering expected when mortality rates are reduced or seasons are lengthened. Under three of these mechanisms (1, 2, 4), persistent selection for early flowering might not be a paradox at all. Instead, what we see as selection for early flowering is in fact only part of the story, and selection at other life stages, in other years, or on correlated traits opposes the widely reported trend. Fluctuating selection over life stages could sum to weakened directional selection, or even stabilizing selection, on lifetime fitness (McGlothlin, 2010). When fluctuations instead occur over generations, population mean flowering time will be constrained within certain limits, as it is under stabilizing selection. Consequences for the amount of variation maintained, allele frequencies, and other parameters, however, differ (Kondrashov & Yampolsky, 1996; Burger & Gimelfarb, 2002). Under the remaining mechanism (3), selection for early flowering is explained as selection on environmental or mutational variance. All four mechanisms are amenable to experimental, statistical, and genetic analysis that can reveal the causes underlying selection for early flowering. Genetically-based studies of selection on flowering time (and duration), experiments extending flowering-time variance, statistical accounting for condition, manipulations of the covariance between flowering time and condition, and long-term pedigree studies of natural populations (modelled after similar work in free-living animals, e.g. Kruuk *et al.*, 2000; Stinchcombe, 2014) are all promising directions forward. Still further insight will be gained through increased attention to selection on flowering-time plasticity (Ehrlén, 2015) and to selection acting through the male component of fitness (e.g. Devlin & Ellstrand, 1990; Austen & Weis, 2016a,b; see Forrest (2014) and Austen *et al.* (2015) for theoretical predictions). Given the central importance of flowering to plant fitness and evolution, and the disconnect between expectations and data, explaining selection for early flowering is imperative for plant evolutionary ecologists.

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Author contributions

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References

Ågren J, Schemske DW. 2012. Reciprocal transplants demonstrate strong adaptive differentiation of the model organism *Arabidopsis thaliana* in its native range. *New Phytologist* **194**: 1112–1122.

Amano T, Smithers RJ, Sparks TH, Sutherland WJ. 2010. A 250-year index of first flowering dates and its response to temperature changes. *Proceedings of the Royal Society B: Biological Sciences* **277**: 2451–2457.

Anderson JT, Gezon ZJ. 2015. Plasticity in functional traits in the context of climate change: a case study of the subalpine forb *Boechera stricta* (Brassicaceae). *Global Change Biology* **21**: 1689–1703.

Anderson JT, Inouye DW, McKinney AM, Colautti RI, Mitchell-Olds T. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society B: Biological Sciences* **279**: 3843–3852.

Anderson JT, Lee CR, Mitchell-Olds T. 2011. Life-history QTLs and natural selection on flowering time in *Boechera stricta*, a perennial relative of Arabidopsis. *Evolution* **65**: 771–787.

Andersson M. 1994. *Sexual selection.* Princeton, NJ, USA: Princeton University Press.

Augspurger CK. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators in *Hybanthus prunifolius* (Violaceae). *Ecology* **62**: 775–788.

Austen EJ, Forrest JRK, Weis AE. 2015. Within-plant variation in reproductive investment: consequences for selection on flowering time. *Journal of Evolutionary Biology* **28**: 65–79.

Austen EJ, Weis AE. 2015. What drives selection on flowering time? An experimental manipulation of the inherent correlation between genotype and environment. *Evolution* **69**: 2018–2033.

Austen EJ, Weis AE. 2016a. The causes of selection on flowering time through male fitness in a hermaphroditic annual plant. *Evolution* **70**: 111–125.

Austen EJ, Weis AE. 2016b. Estimating selection through male fitness: three complementary methods illuminate the nature and causes of selection on flowering time. *Proceedings of the Royal Society B: Biological Sciences* **283**: 20152635–20152639.

Bazzaz FA, Carlson RW. 1979. Photosynthetic contribution of flowers and seeds to reproductive effort of an annual colonizer. *New Phytologist* **82**: 223–232.

Bennington CC, McGraw JB. 1995. Phenotypic selection in an artificial population of *Impatiens pallida*: the importance of the invisible fraction. *Evolution* **49**: 317.

Bonduriansky R, Mallet MA, Arbuthnott D, Pawlowsy-Glahn V, Egozcue JJ, Rundle HD. 2015. Differential effects of genetic vs. environmental quality in *Drosophila melanogaster* suggest multiple forms of condition dependence. *Ecology Letters* **18**: 317–326.

Burger R, Gimelfarb A. 2002. Fluctutating environments and the role of mutation in maintaining quantitative genetic variation. *Genetical Research* **80**: 31–46.

Burgess KS, Etterson JR, Galloway LF. 2007. Artificial selection shifts flowering phenology and other correlated traits in an autotetraploid herb. *Heredity* **99**: 641–648.

Cohen D. 1971. Maximizing final yield when growth is limited by time or by limiting resources. *Journal of Theoretical Biology* **33**: 299–307.

Colautti RI, Ågren J, Anderson JT. 2017. Phenological shifts of native and invasive species under climate change: insights from the Boechera-Lythrum model. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**: 20160032.

Colautti RI, Barrett SCH. 2010. Natural selection and genetic constraints on flowering phenology in an invasive plant. *International Journal of Plant Sciences* **171**: 960–971.

Conner JK. 1996. Understanding natural selection: an approach integrating selection gradients, multiplicative fitness components, and path analysis. *Ethology Ecology & Evolution* **8**: 387–397.

Crow JF, Nagylaki T. 1976. The rate of change of a character correlated with fitness. *American Naturalist* **110**: 207–213.

Delph LF, Ashman T-L. 2006. Trait selection in flowering plants: how does sexual selection contribute? *Integrative and Comparative Biology* **46**: 465–472.

Devlin B, Ellstrand NC. 1990. Male and female fertility variation in wild radish, a hermaphrodite. *American Naturalist* **136**: 87–107.

Dorn LA, Mitchell-Olds T. 1991. Genetics of *Brassica campestris.* 1. Genetic constraints on evolution of life-history characters. *Evolution* **45**: 371–379.

Duffy NM, Bonser SP, Aarssen LW. 1999. Patterns of variation in meristem allocation across genotypes and species in monocarpic Brassicaceae. *Oikos* **84**: 284.

Earley EJ, Ingland B, Winkler J, Tonsor SJ. 2009. Inflorescences contribute more than rosettes to lifetime carbon gain in *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany* **96**: 786–792.

Ehrlén J. 2015. Selection on flowering time in a life-cycle context. *Oikos* **124**: 92–101.

Ehrlén J, Münzbergová Z. 2009. Timing of flowering: opposed selection on different fitness components and trait covariation. *American Naturalist* **173**: 819–830.

Ejsmond MJ, Czarnołęski M, Kapustka F, Kozłowski J. 2010. How to time growth and reproduction during the vegetative season: an evolutionary choice for indeterminate growers in seasonal environments. *American Naturalist* **175**: 551–563.

Ellwood ER, Temple SA, Primack RB, Bradley NL, Davis CC. 2013. Record-breaking early flowering in the Eastern United States. *PLoS ONE* **8**: e53788.

Elzinga JA, Atlan A, Biere A, Gigord L, Weis AE, Bernasconi G. 2007. Time after time: flowering phenology and biotic interactions. *Trends in Ecology & Evolution* **22**: 432–439.

Fitter AH, Fitter RSR. 2002. Rapid changes in flowering time in British plants. *Science* **296**: 1689–1691.

Forrest JRK. 2014. Plant size, sexual selection, and the evolution of protandry in dioecious plants. *American Naturalist* **184**: 338–351.

Fournier-Level A, Wilczek AM, Cooper MD, Roe JL, Anderson J, Eaton D, Moyers BT, Petipas RH, Schaeffer RN, Pieper B *et al.* 2013. Paths to selection on life history loci in different natural environments across the native range of *Arabidopsis thaliana. Molecular Ecology* **22**: 3552–3566.

Franks SJ, Sim S, Weis AE. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences, USA* **104**: 1278–1282.

Geber MA. 1990. The cost of meristem limitation in *Polygonum arenastrum*: negative genetic correlations between fecundity and growth. *Evolution* **44**: 799.

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

Goodwillie C, Kalisz S, Eckert CG. 2005. The evolutionary enigma of mixed mating systems in plants: occurrence, theoretical explanations, and empirical evidence. *Annual Review of Ecology, Evolution, and Systematics* **36**: 47–79.

Grafen A. 1988. On the uses of data on lifetime reproductive success. In: Clutton-Brock TH, ed. *Reproductive success.* Chicago, IL, USA: University of Chicago Press, 454–471.

Griffith TM, Watson MA. 2005. Stress avoidance in a common annual: reproductive timing is important for local adaptation and geographic distribution. *Journal of Evolutionary Biology* **18**: 1601–1612.

Hadfield JD. 2008. Estimating evolutionary parameters when viability selection is operating. *Proceedings of the Royal Society B: Biological Sciences* **275**: 723–734.

Hall MC, Willis JH. 2006. Divergent selection on flowering time contributes to local adaptation in *Mimulus guttatus* populations. *Evolution* **60**: 2466.

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

Hendry AP, Day T. 2005. Population structure attributable to reproductive time: isolation by time and adaptation by time. *Molecular Ecology* **14**: 901–916.

Hodgins KA, Rieseberg L. 2011. Genetic differentiation in life-history traits of introduced and native common ragweed (*Ambrosia artemisiifolia*) populations. *Journal of Evolutionary Biology* **24**: 2731–2749.

Houle D, Morikawa B, Lynch M. 1996. Comparing mutational variabilities. *Genetics* **143**: 1467–1483.

Johansson F, Stoks R, Rowe L, De Block M. 2001. Life history plasticity in a damselfly: effects of combined time and biotic constraints. *Ecology* **82**: 1857–1869.

Kenney A, McKay JK, Richards JH, Juenger TE. 2014. Direct and indirect selection on flowering time, water-use efficiency (WUE, δ^{13}C), and WUE plasticity to drought in *Arabidopsis thaliana. Ecology and Evolution* **4**: 4505–4521.

King D, Roughgarden J. 1983. Energy allocation patterns of the California grassland annuals *Plantago erecta* and *Clarkia rubicunda. Ecology* **64**: 16–24.

Kingsolver JG. 1988. Thermoregulation, flight, and the evolution of wing pattern in pierid butterflies: the topography of adaptive landscapes. *American Zoologist* **28**: 899–912.

Kondrashov AS, Yampolsky LY. 1996. High genetic variability under the balance between symmetric mutation and fluctuating stabilizing selection. *Genetical Research* **68**: 157–164.

Kruuk LEB, Clutton-Brock TH, Slate J, Pemberton JM, Brotherstone S, Guinness FE. 2000. Heritability of fitness in a wild mammal population. *Proceedings of the National Academy of Sciences, USA* **97**: 698–703.

Kudoh H, Kachi N, Kawano S. 2002. Intrinsic cost of delayed flowering in annual plants: negative correlation between flowering time and reproductive effort. *Plant Species Biology* **17**: 101–107.

Kunin WE. 1993. Sex and the single mustard: population density and pollinator behavior effects on seed-set. *Ecology* **74**: 2145–2160.

Kunkel KE, Easterling DR, Hubbard K, Redmond K. 2004. Temporal variations in frost-free season in the United States: 1895–2000. *Geophysical Research Letters* **31**: L03201–L03204.

McGlothlin JW. 2010. Combining selective episodes to estimate lifetime nonlinear selection. *Evolution* **54**: 1377–1385.

McKay JK, Richards JH, Mitchell-Olds T. 2003. Genetics of drought adaptation in *Arabidopsis thaliana*: I. Pleiotropy contributes to genetic correlations among ecological traits. *Molecular Ecology* **12**: 1137–1151.

Mitchell-Olds T, Shaw RG. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution* **41**: 1149–1161.

Mojica JP, Kelly JK. 2010. Viability selection prior to trait expression is an essential component of natural selection. *Proceedings of the Royal Society B: Biological Sciences* **277**: 2945–2950.

Montague JL, Barrett SCH, Eckert CG. 2007. Re-establishment of clinal variation in flowering time among introduced populations of purple loosestrife (*Lythrum salicaria*, Lythraceae). *Journal of Evolutionary Biology* **21**: 234–245.

Morrissey MB, Sakrejda K. 2013. Unification of regression-based methods for the analysis of natural selection. *Evolution* **67**: 2094–2100.

Mosquin T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* **22**: 398–402.

Mountford MD. 1968. The significance of litter-size. *Journal of Animal Ecology* **37**: 363–367.

Munguía-Rosas MA, Ollerton J, Parra-Tabla V, De-Nova JA. 2011. Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured. *Ecology Letters* **14**: 511–521.

Murphy C. 1998. Interaction-independent sexual selection and the mechanisms of sexual selection. *Evolution* **52**: 8–18.

O'Connell LM, Johnston MO. 1998. Male and female pollination success in a deceptive orchid, a selection study. *Ecology* **79**: 1246–1260.

O'Neil P. 1997. Natural selection on genetically correlated phenological characters in *Lythrum salicaria* L. (Lythraceae). *Evolution* **51**: 267–274.

O'Neil P. 1999. Selection on flowering time: an adaptive fitness surface for nonexistent character combinations. *Ecology* **80**: 806–820.

Parachnowitsch AL, Caruso CM. 2008. Predispersal seed herbivores, not pollinators, exert selection on floral traits via female fitness. *Ecology* **89**: 1802–1810.

Pilson D. 2000. Herbivory and natural selection on flowering phenology in wild sunflower, *Helianthus annuus*. *Oecologia* **122**: 72–82.

Price T, Kirkpatrick M, Arnold SJ. 1988. Directional selection and the evolution of breeding date in birds. *Science* **240**: 798–799.

Primack R. 1987. Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* **18**: 409–430.

Rafferty NE, Ives AR. 2011. Effects of experimental shifts in flowering phenology on plant-pollinator interactions. *Ecology Letters* **14**: 69–74.

Rathcke B, Lacey EP. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**: 179–214.

Rausher MD. 1992. The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. *Evolution* **46**: 616–626.

Réale D, Berteaux D, McAdam AG, Boutin S. 2003. Lifetime selection on heritable life-history traits in a natural population of red squirrels. *Evolution* **57**: 2416–2423.

Reyes-Fox M, Steltzer H, Trlica MJ, McMaster GS, Andales AA, LeCain DR, Morgan JA. 2014. Elevated CO_2 further lengthens growing season under warming conditions. *Nature* **510**: 259–262.

Roff D. 1993. *The evolution of life histories*. New York, NY, USA: Chapman and Hall.

Rowe L, Houle D. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society of London B: Biological Sciences* **263**: 1415–1421.

Rowe L, Ludwig D. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology* **72**: 413–427.

Rowe L, Ludwig D, Schluter D. 1994. Time, condition and the seasonal decline of avian clutch size. *American Naturalist* **143**: 698–722.

Sandring S, Ågren J. 2009. Pollinator-mediated selection on floral display and flowering time in the perennial herb *Arabidopsis lyrata*. *Evolution* **63**: 1292–1300.

Schluter D, Nychka D. 1994. Exploring fitness surfaces. *American Naturalist* **143**: 597–616.

Sheth SN, Angert AL. 2016. Artificial selection reveals high genetic variation in phenology at the trailing edge of a species range. *American Naturalist* **187**: 182–193.

Shitaka Y, Hirose T. 1998. Effects of shift in flowering time on the reproductive output of *Xanthium canadense* in a seasonal environment. *Oecologia* **114**: 361–367.

Simonsen AK, Stinchcombe JR. 2010. Quantifying evolutionary genetic constraints in the ivyleaf morning glory, *Ipomoea hederacea*. *International Journal of Plant Sciences* **171**: 972–986.

Sinervo B, McAdam AG. 2008. Maturational costs of reproduction due to clutch size and ontogenetic conflict as revealed in the invisible fraction. *Proceedings of the Royal Society B: Biological Sciences* **275**: 629–638.

Singer MC, Parmesan C. 2010. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**: 3161–3176.

Stearns SC. 1976. Life history tactics: a review of the ideas. *Quarterly Review of Biology* **51**: 3–47.

Stearns SC. 1989. Trade-offs in life-history evolution. *Functional Ecology* **3**: 259–268.

Stiles FG. 1977. Coadapted competitors: the flowering seasons of the hummingbird-pollinated plants in a tropical forest. *Science* **198**: 1177–1178.

Stinchcombe JR. 2014. Cross-pollination of plants and animals: wild quantitative genetics and plant evolutionary genetics. In: Charmantier A, Garant D, Kruuk LEB, eds. *Quantitative genetics in the wild*. Oxford, UK: Oxford University Press, 128–146.

Stinchcombe JR, Rutter MT, Burdick DS, Tiffin P, Rausher MD, Mauricio R. 2002. Testing for environmentally induced bias in phenotypic estimates of natural selection: theory and practice. *American Naturalist* **160**: 511–523.

Stinchcombe JR, Weinig C, Ungerer M, Olsen KM, Mays C, Halldorsdottir SS, Purugganan MD, Schmitt J. 2004. A latitudinal cline in flowering time in *Arabidopsis thaliana* modulated by the flowering time gene *FRIGIDA*. *Proceedings of the National Academy of Sciences, USA* **101**: 4712–4717.

Stock AJ, McGoey BV, Stinchcombe JR. 2015. Water availability as an agent of selection in introduced populations of *Arabidopsis thaliana*: impacts on flowering time evolution. *PeerJ* **3**: e898.

Thomson JD. 2010. Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**: 3187–3199.

Turner KG, Hufbauer RA, Rieseberg LH. 2014. Rapid evolution of an invasive weed. *New Phytologist* **202**: 309–321.

Van Dijk H. 2009. Evolutionary change in flowering phenology in the iteroparous herb *Beta vulgaris* ssp. *maritima*: a search for the underlying mechanisms. *Journal of Experimental Botany* **60**: 3143–3155.

Van Dijk H, Boudry P, McCombie H, Vernet PH. 1997. Flowering time in wild beet (*Beta vulgaris* ssp. *maritima*) along a latitudinal cline. *Acta Oecologica* **18**: 47–60.

Wadgymar SM, Cumming MN, Weis AE. 2015. The success of assisted colonization and assisted gene flower depends on phenology. *Global Change Biology* **21**: 3786–3799.

Wadgymar SM, Daws C, Anderson JT. 2017. Integrating viability and fecundity selection to illuminate the adaptive nature of genetic clines. *Evolution Letters*. doi: 10.1002/evl3.3.

Waser NM. 1978. Interspecific pollen transfer and competition between co-occurring plant species. *Oecologia* **36**: 223–236.

Weinig C, Stinchcombe JR, Schmitt J. 2003. Evolutionary genetics of resistance and tolerance to natural herbivory in *Arabidopsis thaliana*. *Evolution* **57**: 1270–1280.

Weis AE, Wadgymar SM, Sekor M, Franks SJ. 2014. The shape of selection: using alternative fitness functions to test predictions for selection on flowering time. *Evolutionary Ecology* **28**: 885–904.

Willis JH. 1996. Measures of phenotypic selection are biased by partial inbreeding. *Evolution* **50**: 1501–1511.

Wright SW. 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proceedings of the Sixth International Congress of Genetics* **1**: 356–366.

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