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Hard and soft selection on phenology through seasonal shifts in the general and social environments: A study on plant emergence time

Arthur E. Weis,[1,2,3] Kyle M. Turner,[1,4] Bergita Petro,[1] Emily J. Austen,[1] and Susana M. Wadgymar[1]

[1] *Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada*

[2] *Koffler Scientific Reserve at Jokers Hill, University of Toronto, King Township, Ontario, Canada*

[3] *E-mail: arthur.weis@utoronto.ca*

[4] *Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts*

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The timing of transition out of one life-history phase determines where in the seasonal succession of environments the next phase is spent. Shifts in the general environment (e.g., seasonal climate) affect the expected fitness for particular transition dates. Variation in transition date also leads to temporal variation in the social environment. For instance, early transition may confer a competitive advantage over later individuals. If so, the social environment will impose frequency- and density-dependent selection components. In effect, the general environment imposes hard selection, whereas the social environment imposes soft selection on phenology. We examined hard and soft selection on seedling emergence time in an experiment on *Brassica rapa*. In monoculture (uniform social environment), early emergence results in up to a 1.5-fold increase in seed production. In bicultures (heterogeneous social environment), early-emerging plants capitalized on their head start, suppressing their late neighbors and increasing their fitness advantage to as much as 38-fold, depending on density. We devised a novel adaptation of contextual analysis to partition total selection (i.e., cov(ω, *z*)) into the hard and soft components. Hard and soft components had similar strengths at low density, whereas soft selection was five times stronger than hard at high density.

KEY WORDS: Competition, constant yield, contextual analysis, frequency-dependent selection, germination, multilevel selection, phenotypic manipulation, social environment, social selection.

Wallace (1975) coined the term "soft selection" to denote situations where the fitness of an individual depends upon its competitive rank within its local group. A *Drosophila* larva bearing a certain mutation may have high or low fitness in a laboratory vial, he noted, depending on the genotypes of its competitors. When reared with the wild type, it may fail to gain one of the fixed numbers of pupation sites on the vial wall. The same mutant larva, however, would easily obtain a pupation site if competing against genotypes with more deleterious mutations, or in a less crowded vial. Regardless of the genotypic mix and density, each vial (population) yields the same number of adults. The probability of a given genotype being among those successful adults does not depend upon its own merit as measured against a set criterion, but rather as measured against the merit and number of others in its vial. "Hard selection," in contrast, operates independently of population composition. A heat wave selects against low thermal tolerance whether low tolerance is rare or common in the population. If two populations start at equal size, the one with the higher mean tolerance contributes more adults to the mating pool. Christiansen (1975) related the hard/soft selection dichotomy to metapopulation dynamics. If population regulation is local, as when resources limit the number of offspring produced, selection will be soft. Selection is hard under global population regulation, where demes containing more high-fitness individuals contribute more offspring to the next generation.

Theoretical work indicates that hard and soft selection can lead to different evolutionary trajectories. In structured populations, "softer" selection slows the purging of deleterious mutations (Whitlock 2002; Agrawal 2010) affecting mutational load and inbreeding depression. It promotes maintenance of polymorphism through spatial variation in selection (Christiansen 1975, 1985), and accelerates the evolutionary approach to local phenotyic optima (Via and Lande 1985). Goodnight et al. (1992) argued that soft selection is a form of multilevel selection in that an individual's fitness depends both on its own phenotype and on the array of phenotypes in its group.

Importantly, selection on a given trait can have both hard and soft components (Whitlock 2002; Agrawal 2010). A high (low) trait value can enable an individual to meet an extrinsic challenge, but also influence its rank in the local competitive hierarchy. Laffafian et al. (2010) showed that in *Drosophila*, selection against deleterious mutations can fall along a "softness" gradient. This article argues that selection on phenological traits will often have hard and soft components, and presents an experiment on seedling emergence time with several analyses to detect and quantify these components.

HARD AND SOFT SELECTION ON PHENOLOGY

The time of transition to a new life-history phase determines where in the seasonal succession of temporal environments that phase is spent. The date of return by migrant birds to their breeding grounds, or the date of parturition in mammals, affects the synchrony between food resource supply and offspring nutritional demand (e.g., Verhulst et al. 1995; Visser et al. 1998; Réale et al. 2003; Both et al. 2009), which affects breeding success. A pollinator's emergence date determines which floral resources it can access (Mermmot et al. 2007; Forrest and Thomson 2011). A transition made too early or too late in a seasonal environment may expose an individual to frost, seasonal drought, or other unfavorable climatic extremes (Franks et al. 2007; Inouye 2008; Mimura and Aitken 2010). In effect, phenological traits act like habitat choice (Bazzaz 1991; Donohue 2003; Hendry and Day 2005); rather than determining the spatial habitat, they determine which slice of the seasonally shifting environment gets occupied. In this way, hard selection acts on phenology.

The timing of transition also affects exposure to different temporal segments of the *social* environment, and this will generate soft selection. When populations are heterogeneous in phenology, similar individuals are more likely to interact. Asynchronous reproduction, for instance, leads to phenological assortative mating (Weis et al. 2014a) and can generate selection on phenology by limiting mating opportunities for very early and late types (Gerard et al. 2006; Calabrese et al. 2008; Ison and Wagenius 2014; Austen et al. 2015). Intraspecific competitors also can impose selection on phenology (Kokko 1999). When competitive success is size-dependent, later (i.e., smaller) individuals may be disadvantaged, leading to selection for earlier transition—the proverbial early bird gets the worm, denying it to latecomers. Competitive interactions thus generate indirect genetic effects; that is, the phenotype and fitness of a focal individual is influenced not just by its own genotype, but also by the genotypes of the individuals with which it interacts (Wolf et al. 1998, 1999). The change in population mean caused by selection on the direct genetic effect may be opposed by the indirect effect (Griffing 1977; Muir 2005). If, for instance, an early life-history transition causes competitive superiority, early alleles will increase in frequency when rare. As those alleles spread, however, the social environment becomes more competitive, slowing further selection response (Wilson 2014). Fisher (1958) called this "evolutionary environmental deterioration." Clearly, selection through the social environment will be both density- and frequency-dependent, that is, it will be "soft."

Detecting the separate effects of the general and social temporal environments on fitness—the hard and soft selection components—is challenging, as the two environments are necessarily correlated. Not only do early birds always face early-season conditions, they also interact most strongly with other early birds. Revealing their separate effects requires phenotypic and environmental manipulation.

Plant emergence date is an easily manipulated trait that determines *what* the plant interacts with, in terms of spring frost, summer drought, soil resource flux, and exposure to enemies/mutualists/competing species—the general environment. These fitness impacts of emergence time have been studied in a number of species (e.g., Miller 1987; Kalisz 1989; Stratton 1992; Kelly and Levin 1997; Seiwa 2000; Verdú and Traveset 2005). In some cases, a delay in germination can switch a plant from a summer to winter annual, or from an annual to a biennial (Donohue 2002; Donohue et al. 2005; Galloway and Etterson 2007). Emergence date also determines *who* the plant interacts with—the social environment—in terms of intraspecific competition between early and late emergents. Small levels of size variation at the start of the season lead to the formation of competitive size hierarchies (Solbrig and Solbrig 1984; Weiner and Thomas 1986), particularly in monospecific stands. Late emerging seedlings start life at the bottom of the hierarchy so that shading by their early (i.e., larger) neighbors suppresses their growth (Ross and Harper 1972; Howell 1981; Statton 1985; Harmon and Stamp 2002). The early emergents thereby gain an asymmetric competitive advantage.

ESTIMATING HARD AND SOFT SELECTION COMPONENTS

Few attempts have been made to examine the relative strengths of hard and soft selection and these have employed methods that lack either generality or precision. Agrawal and colleagues (Laffafian et al. 2010; Ho and Agrawal 2012) have examined the "softness" of selection against known deleterious mutations in *Drosophila*. These experiments employed a statistical model to estimate the decline in absolute fitness of a mutant genotype when competing with the wild type. The model's "softness" parameter ranges from 0 (pure hard selection) to 1 (pure soft selection). Although quite powerful for the given situation, the model appears limited to traits measured on a binary scale. Others have adapted selection gradient analysis (Lande and Arnold 1983) to compare the strength of selection on plant defense traits in an array of subpopulations, assuming alternative hard and soft selection scenarios (Juenger et al. 2000; Kelley et al. 2005). In both scenarios, the overall selection gradient is taken as the weighted mean of the gradients for each subpopulation. Local mean fitness is included in the weighting scheme for hard selection (i.e., global population regulation), but not for soft selection (all populations make the same per capita contribution to the next generation). Although this compares selection under the alternative scenarios, it does not partition total selection into hard and soft components.

We explored the hardness/softness of selection on emergence time by competing early and late emerging phenotypes in experimental populations that differed in density and phenotype frequencies. The Materials and Methods section describes in more detail our approach to detecting the population-level manifestations of hard and soft selection vis-à-vis population-level reproductive yield and yield inequality within populations. This section presents a new, general method to partition selection into hard and soft components, using contextual analysis (Heisler and Damuth 1987).

The strength of selection acting on a trait can be quantified as the covariance between trait value and relative fitness, that is, cov(ω, z) (Price 1970). This very general relationship applies to any type of "trait," from allele frequency to continuous scale phenotypes, and to levels of selection from genotypes to populations (Wade 1985; Frank 1997; Okasha 2004; Rice 2004). Lande and Arnold (1983) showed that this covariance can be partitioned into the direct effect of trait z on fitness and the indirect effects imposed by traits correlated with z. Contextual analysis is a variant of the Lande–Arnold approach that incorporates indirect effects of group properties on cov(ω, z). Heisler and Damuth (1987) show that group-level terms in contextual analysis are the indirect effects of group selection on individual selection (see Okasha 2004).

Contextual analysis regresses individual relative fitness over both individual phenotype and group characters, such as mean phenotype. The covariance between relative fitness and the phenotype is partitioned into the partial covariances due to individual and group contribution:

$$\mathrm{cov}(\omega_i, z_i) \quad = \quad \beta_1 \mathrm{var}(z_{ij}) \ + \ \beta_2 \mathrm{var}(Z_j), \qquad (1)$$

where z_{ij} is the phenotype of the ith individual in the jth group, Z_j is the mean phenotype of the jth group, and β_1 and β_2 are the partial regression coefficients of relative fitness, ω_i, onto z_{ij} and Z_j, respectively. The first term on the right-hand side denotes the covariance between individual phenotype and fitness, holding the contribution of the group statistically constant. The second term is the effect of group trait on fitness, holding individual contributions constant.

The parameters β_1 and β_2 vary with the intensity of selection imposed by the general and social environments, but they do not directly correspond to hard and soft selection components. Consider the boundary conditions where selection is either purely hard or purely soft. When trait z has no impact on competitive ability, the competitive environment and its effect on fitness does not change with group mean, Z, and so $\beta_2 = 0$. In this case selection on z is purely hard, and its direction and intensity are indicated by the sign and magnitude of β_1.

Under purely soft selection, β_1 and β_2 are both nonzero, and *opposite in sign*. To see why, recall Fisher's concept of evolutionary environmental deterioration. A highly competitive individual gains a fitness advantage by suppressing less competitive neighbors, leading to a *positive* value for β_1. However, that same individual is reciprocally suppressed by highly competitive neighbors. This negative effect of the competitive environment on fitness increases as the population mean competitive ability, Z, increases, that is, β_2 is *negative*. Importantly, Goodnight et al. (1992) discovered that under purely soft selection the individual- and group-level selection gradients are not only of *opposite sign*, but also of *equal absolute value*, that is, $\beta_1 + \beta_2 = 0$.

This equality in absolute value provides the key for partitioning total selection into hard and soft components. If the sum of the two coefficients is not zero, something more than soft selection operates, which by default, is hard selection. Equation (1) can be thus rewritten as:

$$\mathrm{cov}(\omega_i, z_i) = (\beta_1 + \beta_2)\mathrm{var}(z_{ij}) - \beta_2 \mathrm{var}(z_{ij}) + \beta_2 \mathrm{var}(Z_j). \quad (2)$$

The first term on the right-hand side is the portion of selection in excess of soft selection—hard selection. Soft selection is then the *sum* of the second and third terms. The term $-\beta_2\mathrm{var}(z_{ij})$ quantifies the fitness gained when a focal individual suppresses its neighbors, while the term $\beta_2\mathrm{var}(Z_j)$ quantifies the fitness lost when neighbors suppress the focal plant. (N.B. $|\beta_1 + \beta_2| < |\beta_1|$ because β_1 quantifies the selection gradient due to the combined hard and soft components of individual selection, while $\beta_1 + \beta_2$ quantifies the hard component alone.)

Whether soft selection constitutes true group selection is a topic of spirited debate (Wade 1985; Wade et al. 1999; Okasha 2004; Rice 2004; Goodnight 2005; Sober 2011). Regardless of opinion on that matter, our adaptation of contextual analysis separates selection due to the general environment from that due to the social environment.

STUDY GOALS

We performed a phenotypic manipulation experiment to address the following two questions: (1) Do variations in the general and social environments impose a combination of hard and soft selection on seedling emergence time? And, (2) if so, which selection component is stronger? By planting seeds of *Brassica rapa* on two dates, we simulated the advantage of a dominant allele for early emergence over its late allele, randomized over genetic background and environmental maternal effects. The first question is addressed through analyses at both the population and individual levels, with formal statistical tests appropriate to the error distributions of the dependent variables. We then apply equation (2) to describe the effect size of the general and social environments on plant fitness.

Materials and Methods

EXPERIMENTAL SETUP AND DATA COLLECTION

Eighteen experimental populations were established in circular plastic tubs (129 cm in diameter, 24 cm deep) in a 3 × 6 array on an open rooftop at the University of Toronto in June of 2008. Seeds were derived from the "Arboretum" population of the San Diego Creek drainage, Orange Co., California, USA (see Franke et al. 2006; Franks et al. 2007). In its home environment, this species germinates with the start of the rainy season (December) and completes reproduction four to five months later when the annual summer drought begins (Franke et al. 2006). The small bees and flies that pollinate this species (Parker et al. 2015) were observed in abundance on the rooftop, throughout the experiment. We simulated two emergence phenotypes by planting seeds in two cohorts, seven days apart. Five days before a planting, seeds were placed on wet filter paper in covered Petri dishes and stored at 4°C in an illuminated incubator under a 14-h photoperiod. Tubs were planted as monocultures of either the early or late types, or as a 50:50 biculture, resulting in three phenotypic frequencies.

To clarify terminology, the plants within each tub are referred to as a population. Emergence times of early and late types were scored as 0 and 1, respectively. Thus, the frequency of the late type in a population is the same as mean emergence time, that is, $Z_j = 0.0$, 0.5, or 1.0. When referring collectively to the $Z_j = 0.0$ and 1.0 treatment levels, we apply the term "monoculture," while "biculture" is used to contrast the $Z_j = 0.5$ level to the monocultures. A negative covariance between phenotype and fitness denotes selection for early ($z = 0$) emergence.

Phenotypic frequency was crossed with a density treatment (Fig. 1). At low density, seeds were planted in a hexagonal grid with 10 cm spacing. The outer two "rings" in the tub were used as a buffer against edge effects, leaving 31 experimental plants per tub. Seeds were planted at 5 cm spacing in the high-density treatment, with four buffer rings and 113 experimental plants (Fig. 1). In each tub the phenotype frequencies in the buffer matched that for the experimentals. Two seeds were planted at each grid point. The soil surface area occupied by the experimental plants was the same at both densities. Each of the six treatment combinations was replicated three times.

Plantings were monitored daily, and the emergence date of each seedling marked by inserting a color-coded plastic toothpick next to it in the soil. Approximately 80% of plants emerged on the third day after planting, and over 95% by the fifth day. When both seeds at a position emerged, one was removed, alternating between right and left seedlings.

The length and width of the largest leaf were recorded 14 days after planting (early and late types measured one week apart); these were multiplied together to estimate leaf size, referred to as "leaf area-14." As plants senesced, stem diameter (mm) was taken at the lowest leaf scar, and the stem height at the highest. All fruits were then collected and counted.

In monocultures, fitness differences between the early and late phenotypes are attributable to differential impacts of the temporal general environment (hard selection), because all plants grow in a homogenous social environment. The social environment in the bicultures is heterogeneous, which exerts additional (soft) selection.

DATA ANALYSIS

Yield and reproductive inequality in populations

The hard and soft selection components have two predictable manifestations at the population level, as Wallace (1975) and others (Christiansen 1975, 1985; Goodnight 2005) indicated. First, under hard selection, total reproductive yield increases with the frequency of the favored types: the more superior plants there are in a population, the greater their aggregate seed production. Under purely soft selection, in contrast, the increase in individual seed production by the superior type is counterbalanced by reduced production by the inferior type, leaving no correlation between yield per unit area, type frequencies, or starting density. In other words, populations follow the law of constant yield (Donald 1951; Weiner and Freckleton 2010) for reproductive output (Goodnight et al. 1992; Goodnight 2005). We tested for constant yield with a linear model that included terms for phenotype frequency, density, and their interactions. Analysis of residuals did not indicate departures from normality. The analysis included a quadratic term

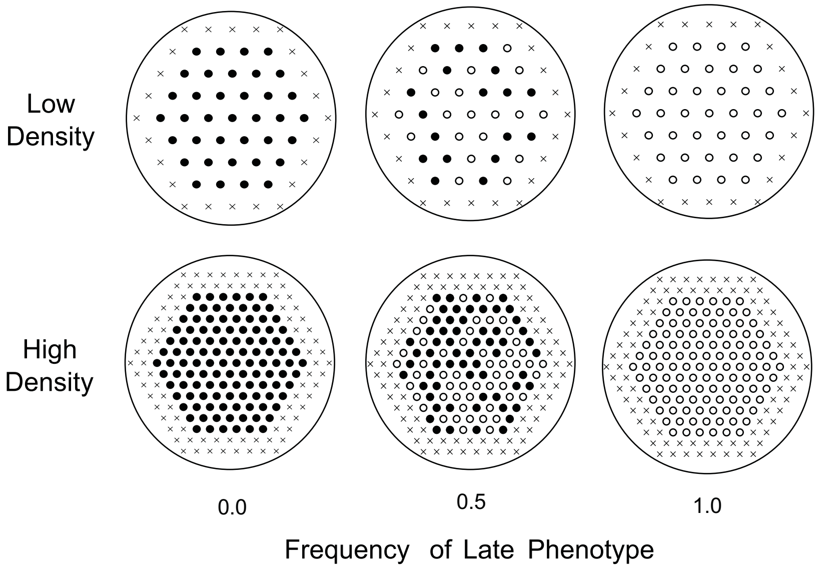

Figure 1. Experimental layout. Symbols as follows: ●, early germinating; ○, late germinating; ×, buffer plants. The frequency of early and late germination in the buffer plants matched that of the frequency treatment level. In the actual experiment, low-density tubs had two buffer rings and the high-density had four. Each of the six treatment combinations were replicated three times.

for frequency, should biculture yield deviate from a linear trend between the two monocultures.

The second manifestation of soft selection concerns fitness variation within populations. In heterogeneous social environments, asymmetric competition between individuals of superior and inferior rank leads to strong reproductive inequality (high variation in fitness). In contrast, reproductive inequality will be lower in homogeneous social environments, where all individuals are of the same competitive rank. Thus, a concave relationship of within-population fitness variation to phenotype frequency indicates soft selection has operated.

We quantified within-population variation in pod production through the Gini coefficient, denoted as G, which measured reproductive inequality as the depth of the Lorenz curve (Damgaard and Weiner 2000, De Maio 2007). This curve plots the cumulative proportion of population total reproductive output over the cumulative proportion of the population considered, when individuals are ordered in increasing value by output. For example, at $x = 1$, y is the number of pods produced by the least fecund plant; at $x = 2$, y is the number produced by the two least fecund plants combined; at $x = 3$, y is the aggregate number produced by the three least fecund, and so on. If all plants had equal pod production, the Lorenz "curve" would be a diagonal straight line, whereas inequality produces a convex curve. G is constructed by first taking the area, A, under the observed Lorenz curve, followed by the area under the diagonal line, B. The coefficient is $G = (B - A)/B$. When $G = 0$, all plants produce the same number of pods. A value of $G = 1$ would result if all pods are produced by a single individual, while the remainder produce none. Economists use the Gini coefficient to characterize income and wealth inequality (De Maio 2007), while plant population biologists use it to measure the strength of competitive size hierarchies (Damgaard and Weiner 2000). G has advantages over other measures of inequality, such as the coefficient of variation, in that it is bounded by 0 and 1, and is less sensitive to outliers (De Maio 2007). We calculated G for the 18 populations with the ineq package in R (R Development Core Team 2008; Zeileis 2013). We tested for a concave relationship of G to phenotype frequencies using the same linear model design as for yield. A significantly negative quadratic term would evidence a population-level manifestation of soft selection.

Impact of general environment on individual size and reproduction

We start our examination of individual fitness by focusing on the monoculture populations. In these homogeneous social environments, all individuals are of the same competitive "rank," and so selection on emergence time has no soft component. Selection occurs because one of the emergence types experiences a superior slice of the temporally shifting environment.

We used a mixed-effects linear model to test for differences between emergence types and densities in leaf area-14, stem diameter, and stem height. Individual germination time (0 vs. 1) and density were fixed effects and tub was a random effect. This was performed using the nlme package in R (Pinheiro et al. 2014). The varIdent command generated a weighting factor that corrected for heterogeneity in the residuals among factor levels (Zuur et al. 2009).

Detecting an effect of general environment on reproductive output required a different model structure. A number of plants failed to reproduce (a few died early, more failed to mature seed), leading to overdispersion of residuals. To accommodate this error structure, we applied a hurdle model (Zuur et al. 2009; Haymes and Fox 2012) that proceeds in two phases. The first phase tested treatment effects on the failure/success of plants to produce at least one pod. The second phase considered only successful plants, and tested the effects of emergence time, density, and their interaction on the number of pods they produced. This was accomplished in the glmmADMB package in R (Bolker et al. 2009, 2012). The phase one analysis assumed a binomial error distribution, whereas phase two assumed a negative binomial distribution truncated below 1. Both phases employed the log link. Models were optimized by dropping nonsignificant terms, using the analysis of variance (anova) function and Akaike information criterion (AIC) values to determine improvement in fit. If the best-fitting model included nonsignificant terms, we retained them. As the test statistic for each fixed effect, we present χ^2 as calculated by the car package (Fox and Weisberg 2010).

Impact of social environment on individual size and reproduction

Early and late plants within the biculture populations would experience not only different general environments, but also a heterogeneous social environment. In other words, selection in these populations can have both hard and soft components. Thus, the appropriate test for soft selection is whether the fitness difference between early and late emergents is amplified (diminished) at intermediate phenotype frequencies, that is, a significant "individual emergence time × population mean emergence time" interaction. The experiment's blocking structure, which was designed for a straightforward analysis of the population-level manifestations of hard and soft selection, and for contextual analysis, complicated tests for this interaction. The problem was that 12 of the 18 experimental tubs contained either all early or all late emergents, and thus the emergence time and population mean treatments were not crossed within all experimental blocks, making block effects uninterpretable. One option was to ignore blocking structure altogether and proceed with a fixed effects model. Instead we chose to re-block the experiment by pairing tubs from the $Z_j = 0.0$ and 1.0 levels (and the same density) into pseudoblocks. For instance, data from tub 3, which had only early plants in low density, were pooled with data from tub 4, which had only late plants, also at low density; these formed pseudoblock A. To the extent possible, we paired tubs with their closest neighbor of the opposite planting date, but same density. Each tub with $Z_j = 0.5$ was treated as its own pseudoblock. This reblocking changed the "population frequency"' to a "population uniformity" term. In all, there were three pseudoblocks for each of the four combinations of the population uniformity and density treatments. Size data were analyzed as a mixed effects model, and seed pod production by a hurdle model, as described above. A significant interaction between individual emergence time and population uniformity supports rejection of the null hypothesis that soft selection is absent. The three-way interaction tests the null hypothesis that population density has no effect on the softness of selection.

Partitioning total selection into hard and soft components

Contextual analysis (described in the Introduction) is based on standard multiple regression; the confidence intervals and statistical tests it produces depend upon normally distributed residuals. The severely overdispersed residuals observed in this experiment, particularly in the high-density bicultures, preclude using contextual analysis for hypothesis testing. Thus, we rely on the mixed-effects hurdle model just described to test null hypotheses on the occurrence of hard and soft selection. We use our modification of contextual analysis solely to describe their effect sizes. Partial regression coefficients of emergence time (β_1), and population mean emergence time (β_2), on relative fitness were obtained with a standard linear model (R Development Core Team 2008). Emergence time was standardized to zero mean and unit variance, and fitness relativized across the entire experiment. Hard and soft selection components were then calculated by multiplying β_1 and β_2 by the individual- and population-level variances in pod production, respectively (eq. 2).

Results

YIELD AND REPRODUCTIVE INEQUALITY OF POPULATIONS

Population yield fell in proportion to the frequency of late plants (Fig. 2A), indicating that late emergers experienced a poorer general environment. Density had no direct effect on the yield of seed pods, although the interaction of density with population mean was marginally significant (Table 1). The slope of yield over the proportion of late emergents, Z, was numerically closer to zero at high density—yield was more nearly constant—which suggests that the component of soft selection might be intensified at high density. Regardless, the significant main effect of phenotypic frequency supports a population-level manifestation of hard selection—the more early emergents, the higher the population yield.

Biculture populations formed significantly stronger size hierarchies than either monoculture (Fig. 2B), evidenced by the highly significant negative quadratic term in the regression of the Gini coefficient over population mean (Table 1). Figure 3 illustrates the Lorenz curve (which the falls along the tops of the black bars) for the populations with the lowest and highest Gini coefficient, which were a $Z_j = 0.0$ low density, and a $Z_j = 0.5$ high

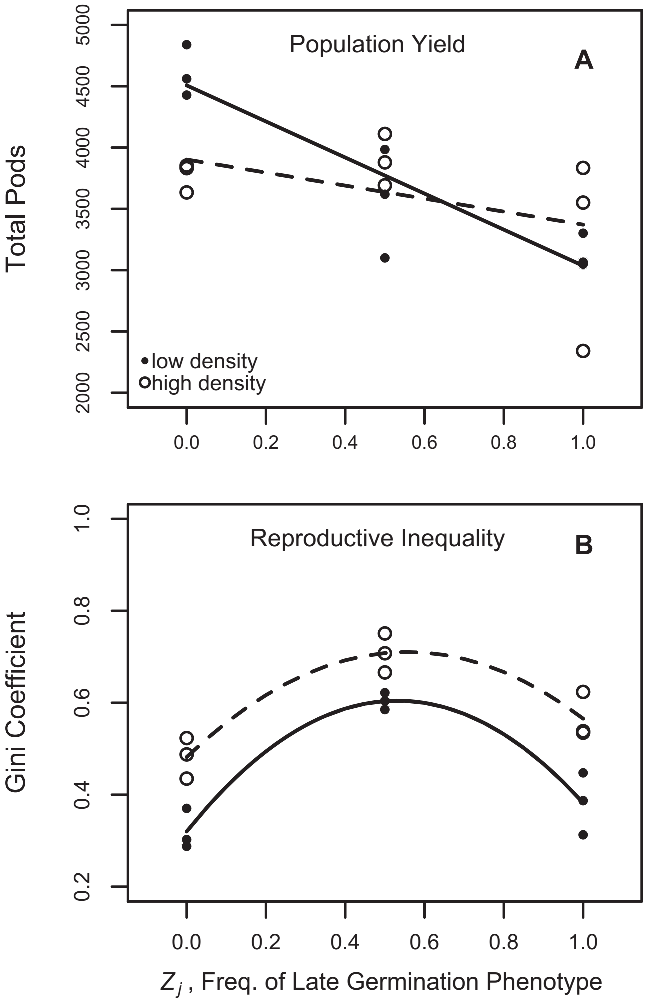

Figure 2. Population yield of seed pods and within-population inequality in seed pod production. (A) Total number of pods produced in the 18 experimental populations, by density and phenotype frequency levels. (B) Gini coefficients for pod production. (C) Symmetry of the Lorez curve. Symmetry levels less than 1.0 indicate that inequality is concentrated toward individuals with low or zero pod production.

density population, respectively. The linear term for the regression was also significant and positive, indicating lower inequality when early emergents compete among themselves, than when late competes with late. Inequality increased significantly with density as would be expected with a more intense competitive environment (Fig. 2B, Table 1). The absence of a significant interaction between the density and frequency terms indicates their effects are additive. The greater inequality in reproduction (fitness) when the two emergence types compete is a population-level manifestation of soft selection.

EFFECTS OF EMERGENCE TIME ON SIZE AND REPRODUCTION IN MONOCULTURE

Similar sizes were achieved by early and late emergents in the monocultures (Fig. 4, Table 2A). The exception was leaf area-14, where the late emergents were approximately 15% larger. Emergence time had no detectable affect on final stem diameter, but a marginally significant increase in final stem height was seen in late populations (Table 2A). These data suggest that the general environment experienced by early and late emergents resulted in only minor differences in growth. High density reduced final size directly, and magnified the effect of emergence time on height differences, as indicated by the significant interaction term.

In contrast to the weak effect of emergence time on plant size, late emergents exhibited a substantial disadvantage in seed pod production in the monocultures (Fig. 5, Table 3A). This fits

Table 1. Response of population characteristics to the frequency of emergence time phenotypes and plant density. *F* ratios are for optimized ANCOVA models.

	F-ratio	
	Population Yield	Gini Coefficient
Phenotype frequency	17.65^{*}	7.16^{*}
Phenotype frequency^2	–	85.53^{***}
Density	0.48 *n.s.*	45.26^{***}
Phenotype frequency × density	$3.89^{\dagger}$	–

$^{***}P < 0.0001$, $^{*}P < 0.05$, $^{\dagger}P < 0.10$

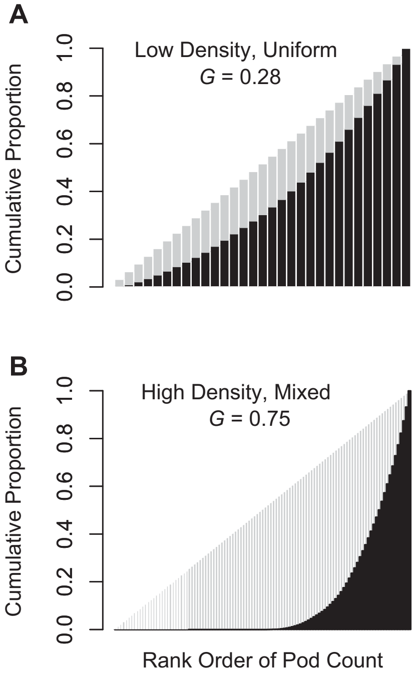

Figure 3. Lorenz curves and Gini coefficients for the populations with: (A) the greatest equality; and (B) the greatest inequality. Lorenz curve lies across the tops of the dark bars. In the case of perfect equality, the Lorenz curve would lie across the tops of the open bars.

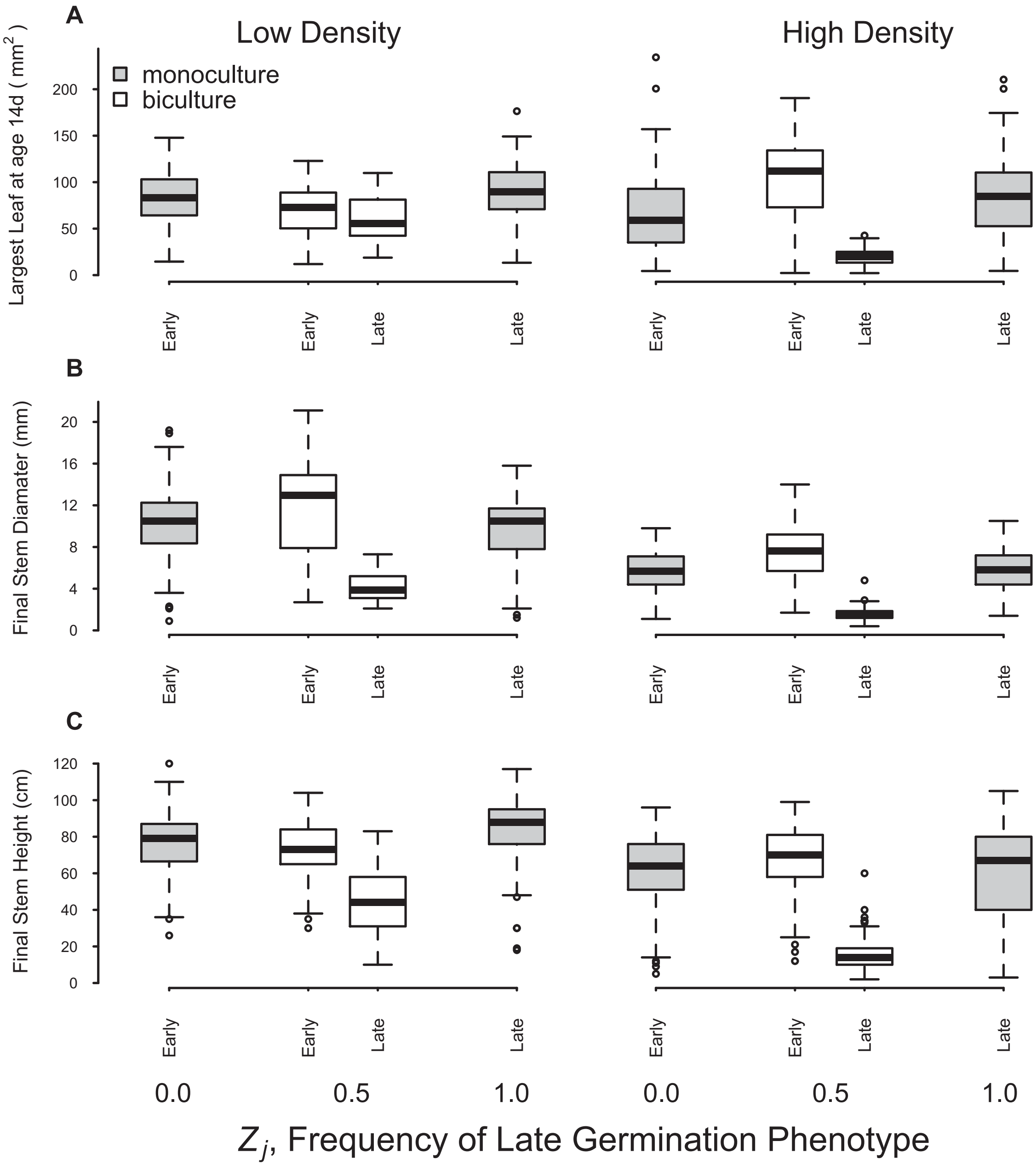

Figure 4. Distribution of three size traits in early and late germinating plants in mono- and biculture, at two densities, indicted by Box plots. (A) Leaf area-14 (the length × width of the largest leaf 14 days after planting). (B) Stem diameter at maturity, measured at the level of the first leaf node. (C) Stem height at maturity measured at maturity at the level of the highest main-stem leaf node.

with the observed reduction in yield with phenotype frequency (Fig. 2A). Late plants failed at seed production more often that early ones (16 and 11% respectively; Table 3A). Density increased the reproductive failure rate, but it did not interact with individual emergence time. Among successful individuals, early emergents produced more seed than late ones (Fig. 5). Early plants enjoyed a 1.46-fold advantage over late at low density (early,$\bar{x} = 148.6$ {SD = 88.2}; late, $\bar{x} = 101.3$ {SD = 70.8}). This advantage diminished to 1.16-fold advantage at high density (early, $\bar{x} = 34.6$ {SD = 30.6}; late, $\bar{x} = 29.7$ {SD = 32.2}). All told, these data indicate that early plants enjoyed a more favorable general environment than late ones, imposing hard selection for early emergence.

EFFECTS OF EMERGENCE TIME ON SIZE AND REPRODUCTION IN MONO- VERSUS BICULTURE

Size comparisons between plants from the mono- and biculture populations revealed a strong competitive advantage to early emergence (Fig. 4, Table 2B) in the biculture populations. The emergence time × population uniformity interaction was

Table 2. Linear model for plant size as affected by emergence time, planting density and the type of population (homogeneous or heterogeneous).

	F-Ratio			
	Degrees of freedom (df)	Leaf area-14	Diameter	Height
(A) Monocultures				
Emergence time[1]	1	33.78***	0.01 *n.s.*	2.57†
Density[2]	1	0.80 *n.s.*	216.11***	128.88***
Emerge time × density[1]	1	5.02*	1.55 *n.s.*	5.92*
(B) Mono- and bicultures				
Emergence time[1]	1	98.47***	186.69***	343.79***
Density[2]	1	1.03 *n.s.*	278.60***	240.86***
Population uniformity[2]	1	7.42*	110.54***	244.80***
Emergence time × density[1]	1	39.08***	6.03*	66.88***
Emergence time × PopUni[2]	1	4442.81***	512.58***	444.39***
PopUni × density[2]	1	0.62 *n.s.*	3.52†	0.79 *n.s.*
EmTime × PopUni × density[2]	1	113.77***	0.96	8.88*

[1] Denominator degrees of freedom: 239 for area-14; 129 for diameter; and, 124 for height.

[2] Denominator degrees of freedom: 8.

***$P < 0.0001$, *$P < 0.05$, †$P < 0.10$.

significant for all three size traits. Significant three-way interactions show that increased density intensifies the differences for leaf area-14 and final stem height (Table 2B). Inspection of Figure 4B and C shows that early emergents grown in biculture were larger than early plants grown in monoculture. These shifts in size with shifts in population uniformity are consistent with asymmetric competition between the early and late plants.

The fitness benefits of early emergence were markedly enhanced in bicultures (Table 3B, Fig. 5). Reproductive failure rates for early and late plants were similar in the monoculture and biculture populations when grown at low density. In contrast, high density led to a decided increase in reproductive failure among late emergents in the bicultures. The early plants maintained a low failure rate of 6% (including 1% preflowering mortality), but failure rate among the late plants soared to 69% (including 23% preflowering mortality). Successful early plants also produced dramatically more seed pods when grown in biculture, while late ones produced many fewer. All told, in low-density bicultures, the early plants produced an average of 218.2 pods ($SD = 123.3$), while late ones produced an average of only 14.2 (SD = 12.5), a 15-fold difference. In high-density bicultures, mean pod production fell to 68.4 (SD = 57.9) for early plants, and 1.7 (SD = 8.1) for late, a 38-fold difference. The highly significant effect of the emergence time × population uniformity interaction on both fitness components (reproductive failure/success, pod count for successful plants) shows clearly that the advantage of early emergence is magnified by their competitive suppression of late emergents (Table 3B). Three-way interactions were not in evidence at this level of replication.

PARTITIONING SELECTION INTO HARD AND SOFT COMPONENTS

We used contextual analysis to partition total selection into hard and soft components. Across all populations, selection favored early emergence (Table 4), with $\mathrm{cov}(\omega_i, z_i) = -0.197$. This would increase the frequency of the early type by about 10% over one generation, if heritability were 1. About two-thirds of total selection is due to the soft component (Table 4), or in other words, it is twice as strong as hard selection. Because the monoculture treatments, by design, eliminated soft selection, we could validate the hard-selection component estimated from the entire experiment against one estimated from the $Z_j = 0.0$ and 1.0 populations alone. The covariance between individual emergence time and relative fitness here was −0.068, the same as estimated for hard selection by equation (2) (Table 4); the covariance between fitness and population mean was zero, also as expected for hard selection. This result supports the proposed partition of the hard and soft components as per equation (2). We repeated the calculation for hard and soft selection components, looking at the low- and high-density populations separately. Overall selection was nearly four times stronger at low density than at high (Table 4). At low density, the soft selection component was slightly stronger than the hard component (−0.247 vs. −0.225). At high density, soft selection was five times stronger than hard (−0.097 vs. −0.023).

Discussion

By emerging on a particular date, a plant "chooses" *what* general environment it develops in, and, *who* among its conspecifics will

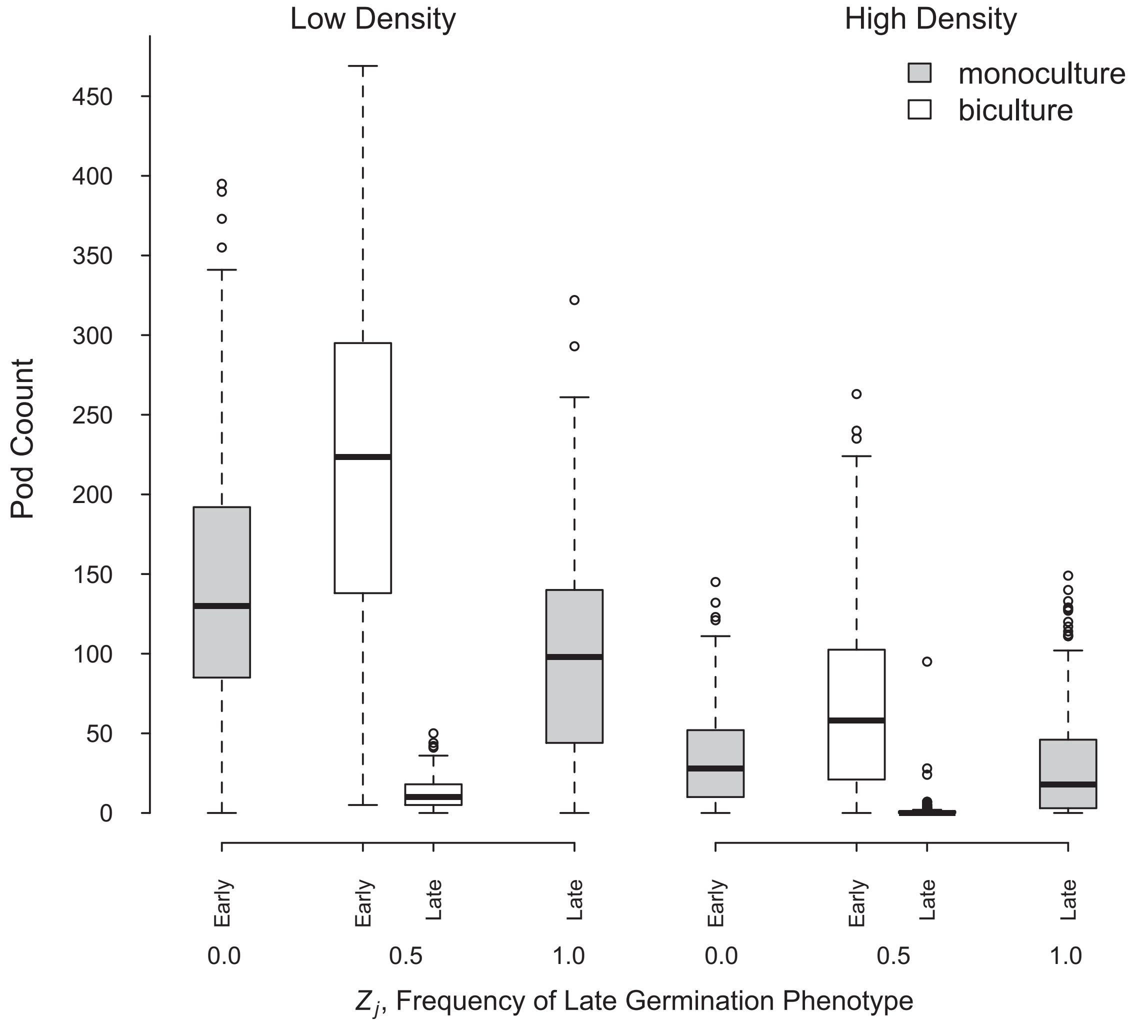

Figure 5. Distribution of seed pods count for early and late germinating plants in mono- and biculture, at two densities, indicted by Box plots.

be its closest competitors. In this experiment, early emergents "chose" the better temporal slice of the general environment. This benefit of being early was amplified when the social environment included late plants. The experimental manipulation of emergence time precludes the possibility that phenotypic selection through the environment is confounded with genetic background or maternal effect. Here, we first discuss the evidence that the general and social environments impose hard and soft selection, respectively. Then, we comment on the potential for contextual analysis to describe the relative strength of the two.

HARD SELECTION THROUGH THE GENERAL ENVIRONMENT

Under purely soft selection, group reproductive yield is unaffected by either the phenotypic distribution within the group or population density. With hard selection, however, group reproductive output rises with the proportion of individuals with high-fitness phenotypes (Christiansen 1975; Wallace 1975; Goodnight et al. 1992; Okasha 2004). The increase in seed yield with the frequency of early plants (Fig. 2A) demonstrates that the general environment imposed hard selection. Considering just the monocultures, across both densities, 50% of the plants were early, but these accounted for approximately 57% of yield. Density did not have a detectable effect on yield, although a marginally significant effect of mean phenotype × density on yield suggests that hard selection may have been stronger at low density. At the individual level, the fitness of early types exceeded that of late plants in the monocultures (Fig. 2A, Table 3A). This advantage came though an increased likelihood of successfully producing at least one pod, and if successful, producing more pods. High density intensified the early advantage in this second component. The partition of total selection as per equation (2) for the two densities further suggests stronger hard selection at low density (Table 4).

What in the general environment increased the fitness of early plants? One possibility would be particularly favorable weather during their first few days of establishment, which would be evidenced by a larger size for early plants at a young age. However, leaf area-14 was slightly smaller in early plants, the reverse of expectation. On another track, pollination could have been more effective during the time interval between the first-flowering dates for early and late plants. Finally, the relevant difference between the general environments of the early and late plants simply could be the duration of favorable growing conditions. In its natural environment, the growing season of the California *B. rapa* source population is terminated by the annual summer drought (Franke et al. 2006; Franks et al. 2007). In this experiment, tubs were watered until nearly all plants senesced, so drought was not a factor. Late summer heat may have been. Early plants may simply have had more time to mature seed before the shift to unfavorable conditions (see Weis et al. 2014b).

SOFT SELECTION THROUGH THE SOCIAL ENVIRONMENT

Asymmetric competition increased reproductive inequality in the bicultures, compared to monocultures (Fig. 2B), indicating a component of soft selection. High density further intensified inequality. Alternatively, higher Gini coefficients for the bicultures could simply be due to the fact that they are mixtures of plants exposed to superior (early) and inferior (late) general environments—asymmetric competition need not be invoked. We examined this possibility by pooling all data from the monocultures, creating a simulated biculture, and calculating its Gini coefficient. At low-density, the Gini coefficient for the simulated biculture was 0.36, which is well below the observed range of values for the actual bicultures, but well within the observed range for the actual monocultures (Fig. 2B, Table 1). At high density, $G = 0.53$, again, well below the observed range for the actual bicultures, but within the range for monocultures. Thus, asymmetric competition, not different general environments, explains the inflated reproductive inequality when early and late plants are grown together.

The hurdle model showed that direct competition increases the difference in pod production between early and late individuals: the emergence time × population uniformity terms are highly significant for both fitness components (reproductive failure/success and pod count; Table 3B, Fig. 5). This confirms statistically that a feature of the population, phenotypic uniformity, influences the covariance between individual phenotype and individual fitness, that is, the selection differential.

PARTITIONING SELECTION INTO HARD AND SOFT COMPONENTS

This experiment showed that plant fitness (through female function) is strongly affected by the slice of the shifting seasonal environment that the plant "chooses." Selection on emergence time has both hard and soft components, imposed by general and social environments, respectively. The first of our motivating questions (are both hard and soft selection in operation?) is answered "yes," based on population- and individual-level analyses. Our second motivating question (which is stronger, hard or soft selection?) was addressed by partitioning the total covariance between emergence time and relative fitness into the partial covariance due to individual and group effects. These calculations suggest that soft selection is the stronger, especially at high density. As Goodnight et al. (1992) discovered, under purely soft selection, contextual analysis yields a partial regression coefficient for individual phenotype over fitness (β_1), that is, equal and opposite of the partial regression coefficient for population mean (β_2). Their interpretation was that with soft selection the indirect effect of group mean on fitness counters the direct effect of individual phenotype. Nonetheless, individual selection predominates total selection, that is, predominates $\mathrm{cov}(\omega_i, z_i)$, because the phenotypic variance of individuals across populations is greater

Table 3. Hurdle regression model of seed pod count as a function of emergence time, planting density, and population uniformity. The regression model first determines if the factors affect whether plants fail to succeed in producing seed pods (zero/nonzero). It then estimates factor effects on the number of seed pods produced for the nonzero seed plants. Results are shown for optimized models (lowest AIC values).

	χ^2	
	Pod production (zero/nonzero)	Number of pods produced (one or more)
(A) Monocultures		
Emergence time	5.10*	9.95**
Density	8.86***	79.59***
Emerge time × density	–	4.16*
(B) Monocultures and bicultures		
Emergence time	51.50***	189.46***
Density	23.93***	114.66***
Population uniformity	8.95**	285.69***
Emerge time × density	–	5.91*
Emerge time × PopUni	55.03***	159.01***
PopUni × density	3.15†	–
EmTime × PopUni × density	–	–

***$P < 0.0001$, **$P < 0.001$, *$P < 0.05$, †$P < 0.10$.

Table 4. **Covariance between individual relative fitness and individual phenotype, decomposed by contextual analysis to components due to variance among individuals within populations and variance among population means. A negative covaraince indicates that early plants (emergence time = 0) produce more pods than late (emergence time = 1).**

	All Populations	Low Density	High Density
(A) Partitioning of total selection			
Total selection: cov(ω_i, z_i)	−0.197	−0.472	−0.120
Hard selection: ($\beta_1 + \beta_2$)var(z_{ij})	−0.068	−0.225	−0.023
Soft selection: $-\beta_2$var(z_{ij}) + $\beta_2$var(Z_j)	−0.129	−0.248	−0.172
(B) Partitioning of soft selection			
Suppression of neighbors by focal: $-\beta_2$var(z_{ij})	−0.387	−0.743	−0.292
Suppression of focal by neighbors: $\beta_2$var(Z_j)	0.258	0.495	0.120

than variance in population means, that is, var(z_{ij}) $>$ var(Z_j) (see eq. 1).

Why is a tool developed to quantify multilevel selection applicable to seedling emergence time? The answer becomes clear when one recognizes that selection on emergence time arises, in part, from asymmetric competition, and asymmetric competition is the reverse of altruism. A focal individual with an "altruist phenotype" suffers a fitness cost to itself while imparting a fitness benefit to its neighbors. In turn, the focal individual gains a fitness benefit by interacting with altruistic neighbors. When the frequency of altruists is high, the individual cost is overcome by the benefit of being in a predominantly altruistic group. In contrast, early emergence confers an individual benefit. An early focal plant gains a disproportionate share of resources by suppressing neighbors. But when the neighbors are also early, they impose a reciprocal suppressing effect on the focal plant, diminishing its fitness. As with an altruistic trait, net selection on emergence time rests on the balance between the fitness effects of individual and group mean phenotypes. The opposition of direct individual selection for competitive suppression of neighbors to the indirect associative effects at the group-level has long been recognized by plant and animal breeders (Allard and Adams 1969; Griffing 1977; Muir 2005). The conflicting effects on fitness are demonstrated for our experiment through the partitioning of soft selection in Table 4B. The partial covariance between emergence time and fitness is negative (early plants favored) and stronger than the positive partial covariance between group mean and individual fitness (a high frequency of early, competitive plants reduces fitness for all).

Although contextual analysis can separate the hard and soft selection components, the data in this particular case strongly violated the statistical assumptions of multiple regression, precluding calculation of standard errors and significance testing through this method. Other procedures, such as aster analysis (Shaw and Geyer 2010) may be adaptable to allow statistical testing of individual and group partial regression coefficients when data are severely overdispersed. Making such adaptations would be a welcome addition to selection analysis.

Intraspecific interactions may affect selection on a wide variety of traits, leading to a component of soft selection. For instance, the probability of being infected/parasitized can depend on the distribution of resistance levels in a population (Carius et al. 2001), and further, competition between affected and healthy individuals can magnify the fitness impact of an attack (Lively et al. 1995: Juenger et al. 2000; Weis and Hochberg 2000; Kelley et al. 2005). A partitioning of total selection into hard and soft components can lead to insights on the role of group attributes to the evolution of resistance, tolerance, and potentially many other traits.

Finally, much recent work has considered the impact of climate change on the evolution of phenological traits (Franks et al. 2007; Bradshaw and Holzapfel 2008; Hoffman and Sgro 2011, Anderson et al. 2012). We reiterate our point that phenological traits determine an individual's exposure to both the general and social environments. Clearly, an extended growing season can shift the optimal transition date between life stages (Bradshaw and Holzapfel 2001; Visser et al. 2004; Anderson et al. 2012; Weis et al. 2014b) in a way that is independent of population composition or density—hard selection. However, an individual's fitness may depend not on just its own phenotype, but the phenotypes and the number of conspecifics interacting with it. Rising temperatures and altered precipitation can affect the composition and size of populations, and so some part of the selection imposed by climate change will come through the soft component. The predictive value of studies anticipating the evolutionary impact of climate change on phenology will increase if these studies account for the frequency- and density-dependence of selection intensity.

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DATA ARCHIVING

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