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The triple helix of *Plantago lanceolata*: Genetics and the environment interact to determine population dynamics

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Abstract. The theory of evolution via natural selection predicts that the genetic composition of wild populations changes over time in response to the environment. Different genotypes should exhibit different demographic patterns, but genetic variation in demography is often impossible to separate from environmental variation. Here, we asked if genetic variation is important in determining demographic patterns. We answer this question using a long-term field experiment combined with general linear modeling of deterministic population growth rates (λ), deterministic life table response experiment (LTRE) analysis, and stochastic simulation of demography by paternal lineage in a short-lived perennial plant, *Plantago lanceolata*, in which we replicated genotypes across four cohorts using a standard breeding design. General linear modeling showed that growth rate varied significantly with year, spatial block, and sire. In LTRE analysis of all cohorts, the strongest influences on growth rate were from year $\times$ spatial block, and cohort $\times$ year $\times$ spatial block interactions. In analysis of genetics vs. temporal environmental variation, the strongest impacts on growth rate were from year and year $\times$ sire. Finally, stochastic simulation suggested different genetic composition among cohorts after 100 years, and different population growth rates when genetic differences were accounted for than when they were not. We argue that genetic variation, genotype $\times$ environment interactions, natural selection, and cohort effects should be better integrated into population ecological studies, as these processes should result in deviations from projected deterministic and stochastic population parameters.

Key words: cohort effect; demography; life table response experiment (LTRE); phenotypic plasticity; Plantago lanceolata; *population dynamics; population projection matrix model; stochastic growth rate.*

Introduction

Wild populations are strongly influenced by the magnitude and variability of environmental factors, such as precipitation and nutrient levels. Natural selection is the differential success of individuals in dealing with these and other factors (Darwin 1859). When this differential success among individuals is at least partially based on the differential success of different genotypes, natural selection can lead to evolution (Lynch and Walsh 1998). With fitness defined in terms of mortality and reproduction schedules, demography provides a link between evolution via natural selection and population dynamics (Kokko and López-Sepulcre 2007, Metcalf and Pavard 2007, Schoener 2011). However, analyses of the dynamics of wild populations typically attribute all or most demographic variation to environmental influences without considering variation in expression of demographic patterns among genotypes and potentially other factors tied to the intrinsic properties of the organism.

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Demographic variation is strongly determined by temporal and spatial environmental influences in wild populations (May 1973). Temporal variation in demographic parameters reflects the influence of climatic trends and processes at the ecosystem level and higher (Kerkhoff and Ballantyne 2003). Such variation impacts life histories by favoring the evolution of traits that minimize negative fitness effects, such as bet-hedging traits (Philippi and Seger 1989). On the other hand, spatial environmental variation is caused by an inconsistent matrix in which organisms live, and impacts life histories by favoring the evolution of spatial sampling strategies, such as propagule dispersal and migration (Gros et al. 2006).

The measurement of temporal and spatial environmental variation in demographic rates is confounded by variation in intrinsic factors. Here, intrinsic factors are those that originate in the biology of the organism rather than in conditions outside of the organism. Genetic variation is difficult to separate from spatial environmental variation because the former is distributed nonrandomly across space (Vekemans and Hardy 2004). Although environmental variation is deemed more important than genetic variation in many demographic analyses of wild populations (Beissinger and Westphal 1998), natural selection can induce evolution

quickly in the wild (Reznick et al. 1997), resulting in strong changes in genetic composition and altered demographic patterns (Bennington and McGraw 1995*a*). Moreover, temporal environmental variation may also confound the observation of intrinsic influences on demographic variation. For example, age-based variation is difficult to separate from temporal environmental variation because not only is age often an unknown in many organisms, but individuals at similar ages also have typically experienced similar environments (Roach 1993). Temporal patterns observed may relate to differing responses by individuals at different ages, impacts of birth in particular periods, and interactions with environmental factors (Holford 1983). Further, temporal environmental variation may confound the observation of genetic influences, particularly when the same genotype exhibits different phenotypes under different environmental conditions (Via et al. 1995). The use of multiple cohorts with mixed genotypes in each one provides a means to separate temporal environmental impacts from intrinsic sources of variation in demographic responses (cf., Roach et al. 2009). A proper breeding design allows genetic variation to be parsed out from other sources of phenotypic variation.

Population projection models are a cornerstone of conservation and evolutionary biology (Menges 2000, Caswell 2001, Beissinger 2002). These analyses rely on annual estimates of mortality, recruitment, and transitions among life history stages calculated for a particular monitoring period (Tuljapurkar et al. 2009), and are used to derive estimates of population growth rate, stable age/stage distribution, extinction probabilities via both deterministic and stochastic analyses, sensitivities of fitness to specific demographic parameters, and other estimates (Beissinger and Westphal 1998, Caswell 2001). Evolutionary and conservation biologists in particular often focus on fitness or population growth rate, respectively, with interest in how major life traits and transitions affect these parameters (Benton and Grant 1999). However, the generality of population projection models may be limited particularly by their robustness to a critical assumption: that the study population will respond in the same way to the same environmental conditions over time. A population's responses to the environment may change over time for several reasons. First, over time natural selection may favor genotypes with different reaction norms from those dominating the population at the time of monitoring. The result could be increasingly different vital rates across time due to an increasingly different genetic composition over time elapsed since the monitoring period (i.e., genetic heterogeneity, per Bennington and McGraw 1995*b*). Second, population-level response to environmental factors can change if the expression of genotypes changes with environment and is partially dependent on conditions experienced during sensitive life stages. The best example is the juvenile stage, during which environmental conditions can partially determine traits in the organism's later life (Knudsen 1998, Nussey et al. 2006), including the age and amount of first flowering (Shefferson and Roach 2010), and even the onset and rate of senescence (Roach 1986, Metcalfe and Monaghan 2001).

Here, we used a long-term (10 years), large-scale demographic experiment of the ribwort plantain, *Plantago lanceolata*, to assess the impacts of environmental and genetic variation in demographic parameters on population dynamics relative to spatial and temporal environmental variation. We report on over 7000 individuals planted in four cohorts over three years. The experimental design included a replicated genetic composition for each cohort, and individuals were planted randomly with respect to space, parentage, and cohort, giving us the power to distinguish genetics from environment. First, we asked whether cohorts planted in different years can exhibit different population dynamics even if they have the same genetic composition at their start, suggesting a strong influence of age or early-life environment. Second, we asked whether population dynamics can vary by genotype, and whether genotypes can exhibit different demographic behavior as the environment changes. Finally, we asked whether genetically variable demographic patterns may lead to different projected population dynamics over time from those projected during the monitoring period, using stochastic simulations.

Methods

Study organism and field methods

Plantago lanceolata L. (Plantaginaceae) is a short-lived, polycarpic perennial dicot with a widespread, holarctic distribution. It is commonly found in disturbed habitats, including mown fields and roadsides (van der Aart and Aulto 1992), and competes poorly in low light (van Tienderen and van der Toorn 1991). The plant produces a basal rosette that persists year-round. Size is very plastic, and individuals of the same cohort show large variation in size (Roach and Gampe 2004). Depending on environmental conditions, plants may increase or decrease in size from year to year (Roach et al. 2009), thus growth patterns provide no clue as to the age of plants. This species is primarily wind-pollinated. In central Virginia, flowering may occur from April to September, though May to August is most common, and inflorescences may be formed by the same individual multiple times per breeding season. Although reproduction may occur in many years throughout the lifetime of the plant, a high proportion of individuals reproduce only once at this field site (Shefferson and Roach 2010). Seed dormancy has been noted (van Groenendael and Slim 1988); however, in a related study in our field site, we found no evidence for dormancy. The life span of individuals conditional on reaching the first reproductive event ranges from 29 to 42 months across cohorts in this study.

This study took place in an experimental field plot at the Shadwell Preserve of the Jefferson Monticello Foundation in Virginia, USA. Monthly temperatures at this site vary from approximately −5°C in the winter to 22°C in the summer, and there is spatial heterogeneity in soil moisture and light levels across the plot (D. Roach, *unpublished data*). At this site, a large natural population of *Plantago lanceolata* (hereafter, *Plantago*) exists and was used as the source of the parental plants used in this experiment. We used a modified North Carolina II breeding design with a total of 20 sire genotypes, 10 dam genotypes, and 40 dam–sire combinations (Lynch and Walsh 1998). This design was repeated for each cohort. Seeds were planted in the greenhouse, and raised, planted in the field, and marked as described elsewhere (Roach 2003). Seedlings of uniform age (approximately six weeks) were planted 15 cm apart in rows each 20 cm apart. This spacing was sufficient to avoid competition between study individuals and is within the natural density of the field. Seedlings were planted in the field in a randomized block design with replication of genotypes and cohorts within 1×14 m sections, which were separated by 1 m to allow researchers to measure plants while minimizing disturbance. Four adjacent sections constituted a block, and here we use data on 12 of the 18 main blocks as the remaining six blocks were only used in certain cohorts. The total planting area was approximately 75×45 m^2. These plantings occurred within, and with minimal disturbance to, the natural plant community, in order to keep ecological interactions as they would be in a wild population. The different cohorts were planted as follows: cohort 1, October 2000; cohort 2, October 2001; cohort 3, April 2002; and cohort 4, October 2002. Here, cohorts 1, 2, and 4 allowed us to assess the impact of annual environmental variability, while cohort 3 allowed us to assess the impact of seasonal environmental variability. This study includes data from the time of planting until December 2009. Although the total number of individuals planted approaches 30 000, only those individuals for which size was consistently measured were analyzed here (cohort 1, 3058 plants; cohort 2, 2803 plants; cohort 3, 1073 plants; cohort 4, 528 plants).

Analytical methods

Population projection modeling.—We defined eight life cycle stages: seedling, tiny adult (≤5 basal leaves), small adult ($5 < x \leq 15$ basal leaves), small-medium adult ($15 < x \leq 25$ basal leaves), medium adult ($25 < x \leq 50$ basal leaves), medium-large adult ($50 < x \leq 75$ basal leaves), large adult ($75 < x \leq 100$ basal leaves), and giant adult (>100 basal leaves). We used eight classes to avoid bias due to low matrix dimensions (Salguero-Gómez and Plotkin 2010), and assigned these particular size classes on the basis of an examination of sizes extant during a sampling of years in the study as well as knowledge of the biology of the plant (we initially based these on quartiles for cohorts 1 and 4 in years 2002–2004, but noted that most plants had fewer than 25 leaves in any given year, and so adjusted size classes to reflect the large amount of data in this group). Plants were assigned to each of these classes on the basis of size measurements taken every November. Plants could be in any adult size class in any particular year regardless of previous size (Appendix A), because aboveground size fluctuates strongly with environment in this and other herbaceous perennials (Roach et al. 2009). We estimated annual mortality as the proportion of individuals alive in April of year t that were still alive in April of year $t + 1$, because reproduction typically occurred after the April census. We used April as the cut-off month in mortality estimates of cohort 3 as well, even though this cohort was planted in a different month (April) than the other cohorts (October), in order to keep cohorts as comparable as possible. For further details on vital rate estimation, see Appendix B.

We constructed population projection models to test the influence of environment via both temporal and spatial variation. We used the aforementioned vital rates to create specific matrix models for each block × year combination within each cohort using the *projection.matrix* function in the *popbio* package in R (Stubben and Milligan 2007, R Development Core Team 2010), covering all years for which all four cohorts were in the field and no longer included seedlings (April 2003–2009). We also constructed reference matrices as element-by-element averages among all matrices. To assess the influence of genetics, we then repeated the same procedure to estimate matrices for all combinations of year and sire in cohorts 1 and 4. Cohorts 1 and 4 were chosen because they are the oldest and youngest cohorts, respectively. In both cases, all full years were used (2001–2009 in cohort 1, and 2003–2009 in cohort 4), and two separate reference matrices were estimated using data within, not among, each of the two cohorts. We did not include growth and mortality occurring in the ~6 months between planting and April in cohorts 1, 2, and 4, and did not include the first year of life following planting in April 2002 in cohort 3. In this evaluation of genetics, we assessed the influence of year but not block because the former exhibited the strongest influence on demography in the four-cohort analysis (see *Results*). For further details on population projection models, see Appendix B.

General linear modeling of population growth rate (λ).—We tested for significant differences in projected population growth rates (λ) among cohorts, spatial blocks, and years in the all-cohort matrix set, and among paternal lineages and years in the cohort 1 and cohort 4 matrix sets, using general linear modeling. We used the *popbio* package in R to obtain λ, the dominant eigenvalue of each matrix, using the lambda function. Then, we analyzed the projected estimates of λ as a

function of all factors using general linear modeling in SPSS PASW Statistics 18.0 (SPSS 2010). Here, cohort was treated as a fixed factor while all other factors (year and block in the four-cohort analysis, sire and year in the one-cohort analyses) were treated as random. In the four-cohort analysis, we included only two-way interactions as there was only one data point per cohort × block × year combination. For the same reason, we did not include the two-way sire × year interaction in either of the single-cohort analyses.

Life table response experiment (LTRE) analyses.—The GLM of λ in each case was designed to test for differences in λ among components of the population, but not for the changes in matrix elements that cause those differences. To identify shifts in projection matrix elements associated with the impacts of tested factors on λ, these matrices were then used in a factorial, fixed-design life table response experiment (LTRE) (Caswell 2001). We tested the same factors in these analyses as in the corresponding GLMs, and all LTRE analyses were conducted via the *LTRE* function in the *popbio* package in R (Stubben and Milligan 2007, R Development Core Team 2010). In the four-cohort case, the factors tested included cohort, year, and block, and all interactions including cohort × spatial block × year, and the reference matrix was the average matrix for all years 2003–2009 in all cohorts and blocks. We also conducted LTREs of sire, year, and sire × year in the matrix sets for cohorts 1 and 4 using the average matrix for all years and sires within each respective cohort as the reference matrix. Here, each cohort was analyzed separately. We estimated the impacts of particular factors on λ by summing the appropriate matrix elements in the resulting LTRE matrices. For example, the impact of the year 2003 on Δλ in the four-cohort analysis was estimated as the sum of LTRE contributions in the average 2003 matrix. We also estimated the impact of each factor on Δλ via fertility, progression, stasis, and retrogression transitions, by summing all LTRE scores corresponding to the appropriate transitions. In addition, we assessed the potential impact of age by looking for common patterns in LTRE scores across time and cohort in all three LTRE analyses. For further details on LTRE analysis, see Appendix B. Finally, because we were concerned that our estimates of fertility and transition probability from seedling to all adult classes might be too high, we repeated the LTRE analysis of cohort 1 first with all fertilities halved, and second with all transitions from seedling to adult size classes halved, but found no substantive differences in the results (Appendix C).

We estimated standard errors for all estimated LTRE effects by bootstrapping 1000 replicates of each data combination from the original demographic data sets in R. The standard error for any particular value was then estimated as the standard deviation of the equivalent value among these bootstrapped data sets. Significant LTRE effects were inferred if the 95% confidence interval ($z = 1.96$) did not overlap with zero.

Stochastic projections.—We conducted a simulation exercise to determine whether differing demographic patterns among paternal lineages could lead to genetic heterogeneity over time and impact demographic projections via stochastic projections of the sire × year matrices from cohorts 1 and 4. First, we estimated stochastic growth rates ($a = \log \lambda_S$) in each case using the *stoch.growth.rate* function in the *popbio* package in R (Stubben and Milligan 2007, R Development Core Team 2010). We developed stochastic projections by randomly drawing years from those observed 100 times with replacement out of eight and six years for cohorts 1 and 4, respectively. Beginning each simulation with equal numbers of individuals corresponding to each paternal lineage in each cohort, we then projected the stage distribution of each paternal lineage year-by-year up to 100 years forward in time using the lineage-specific matrices corresponding to each randomly sampled year. We then estimated the proportion of the cohort composed of each paternal lineage at that projected point in time. To address whether altered genetic composition would result in changed population dynamics within each cohort after 100 years, we also created mean matrices for each cohort for each of the years 96–100 in this simulation, based on the total numbers of individuals projected in each stage regardless of paternal lineage, and estimated the stochastic growth rate (λ_S) for these average matrices based on these five years. This entire process was repeated 1000 times with a different random draw of 100 years each time to estimate mean and standard error lineage proportions and stochastic growth rates. We hypothesized that G × E interactions would lead to significantly different genetic composition after 100 years, and that this genetic heterogeneity would yield significantly different stochastic growth rates from those projected in the original data set.

Results

GLMs of growth rates

Spatial and temporal environmental variation, and genetics, strongly influenced patterns in population growth rates (λ) among cohorts. Population growth rate was typically high, ranging from 0 to 10.8 among cohort × block × year combinations in the four-cohort data set, and from 0 to 12.1 and 2.7 to 9.7 among sire × year combinations in the cohort 1 and cohort 4 data sets, respectively (Appendix D). Here, zeroes were attributed to combinations that died off within the study. In the four cohort data set, year and spatial block significantly influenced λ, while cohort influenced temporal and spatial patterns in λ via interactions with year and spatial block (Table 1). In both one-cohort data sets, λ was significantly determined by sire and year (Table 1), suggesting strong genetic and G × E variation in demographic patterns.

TABLE 1. Importance of factors in general linear modeling and LTRE analysis of population growth rate (λ) in an experimental population of *Plantago lanceolata* at Shadwell, Virginia, USA: (a) all cohort analyses, (b) analyses of cohort 1 only, (c) analyses of cohort 4 only.

Factor	*F*	df	*P*	LTRE variation explained (%)
a) Cohort	1.07	3, 38	0.374	3.4
Spatial block	2.26	11, 34	0.034	7.4
Year	21.16	5, 16	0.001	18.1
Cohort × block	9.35	33, 165	0.001	8.1
Cohort × year	7.87	15, 165	0.001	6.5
Block × year	1.23	55, 165	0.166	28.3
Cohort × block × year	not in GLM	not in GLM	not in GLM	28.3
b) Sire	4.79	19, 133	0.001	13.9
Year	122.12	7, 133	0.001	68.2
Year × sire	not in GLM	not in GLM	not in GLM	17.9
c) Sire	3.74	19, 95	0.001	20.7
Year	62.79	5, 95	0.001	55.3
Sire × year	not in GLM	not in GLM	not in GLM	24.1

Note: All factors were treated as random except cohort, which was treated as fixed.

LTRE patterns

LTRE analysis of the four-cohort data set revealed that temporal environmental variation, and to a lesser extent spatial environmental variation and early-life environment, were strongly influential to population dynamics. Year was most strongly associated with changes to λ, followed by block, and finally cohort (Table 1; Appendix E). Interactions among environmental factors were strongly influential on demographic dynamics. The strongest impacts in terms of magnitude were year × block and cohort × year × block (Table 1; Appendix E). Similar general patterns among cohorts in cohort × year LTRE contributions from 2003 to 2009 suggested that annual patterns in demography were unlinked from age (Appendix E), and so cohort effects are most likely due to different early-life environments among cohorts.

Single-cohort LTRE analysis revealed that population dynamics in *Plantago* varied strongly as a function of genetic makeup and genetic interactions with environment. Paternity, year, and their interaction influenced λ. The strongest LTRE contributions were associated with year in both cohorts, but sire and sire × year were also important (Fig. 1, Table 1). Particular sires had strong deviations from mean λ in both cohorts, while many did not. Intriguingly, year × sire interactions varied with cohort, suggesting a cohort-based context to gene-by-environment interactions determining the expression of demographic traits (Fig. 1, Table 1).

The impacts of sire and year on λ varied across demographic processes and life cycle classes. Fertility was the most influential parameter on λ, as assessed via the impacts of naturally occurring variation in demographic parameters via LTRE analysis. Across cohorts, years, and sires, variation in fertility impacted λ across a range of life stages, most notably the small class (5–15 leaves; Fig. 2a, e, i; Appendix F). Progression from the seedling stage was secondarily influential after fertility (Fig. 2f; Appendix F). In cohort 4, stasis in the small class also appeared to be influential in terms of sire and sire × year variation (Appendix F), while this transition was not influential in cohort 1 (Fig. 2c, g, k). Retrogression was the least influential transition on λ (Fig. 2d, h, l; Appendix F).

Stochastic simulation of cohorts 1 and 4

Stochastic simulation of the demographic patterns measured in cohorts 1 and 4 led to dramatically different projections of both genetic composition and λ over time. After a simulation of 100 years, ~87% of cohort 1 was composed of individuals derived from sires 84 and 102, and sire 124's lineage was extinct in all replicate simulations (Fig. 3). In cohort 4, ~80% of the cohort was composed of individuals derived from sires 22 and 26, which in cohort 1 composed only ~0.6% after 100 years (Fig. 3). These sires generally exhibited relatively high λ each year in their cohorts, with lower variability from year to year than most other sires (Appendix D), resulting in the highest stochastic growth rates among sires within their cohorts. Stochastic simulations of cohort mean matrices corresponding to years 96–100 in the paternal lineage-based simulations led to stochastic growth rates of $a = 2.09 \pm 0.01$ and 1.98 ± 0.01 for cohorts 1 and 4, respectively. In contrast, stochastic simulation of the original matrices without accounting for differential demography among genotypes led to different stochastic growth rates of $a = 2.23 \pm 0.01$ and 2.01 ± 0.01 for cohorts 1 and 4, respectively.

DISCUSSION

Our field-based experiment offers a novel approach to separate genetic from spatial and temporal variation in demographic processes, and our GLM and LTRE analyses found all to be important and interactive. Most interestingly, population dynamics were genetically variable, and the demographic response of genotypes varied among cohorts, suggestive of the strong influence of early-life experience on later-life demography. Plastic

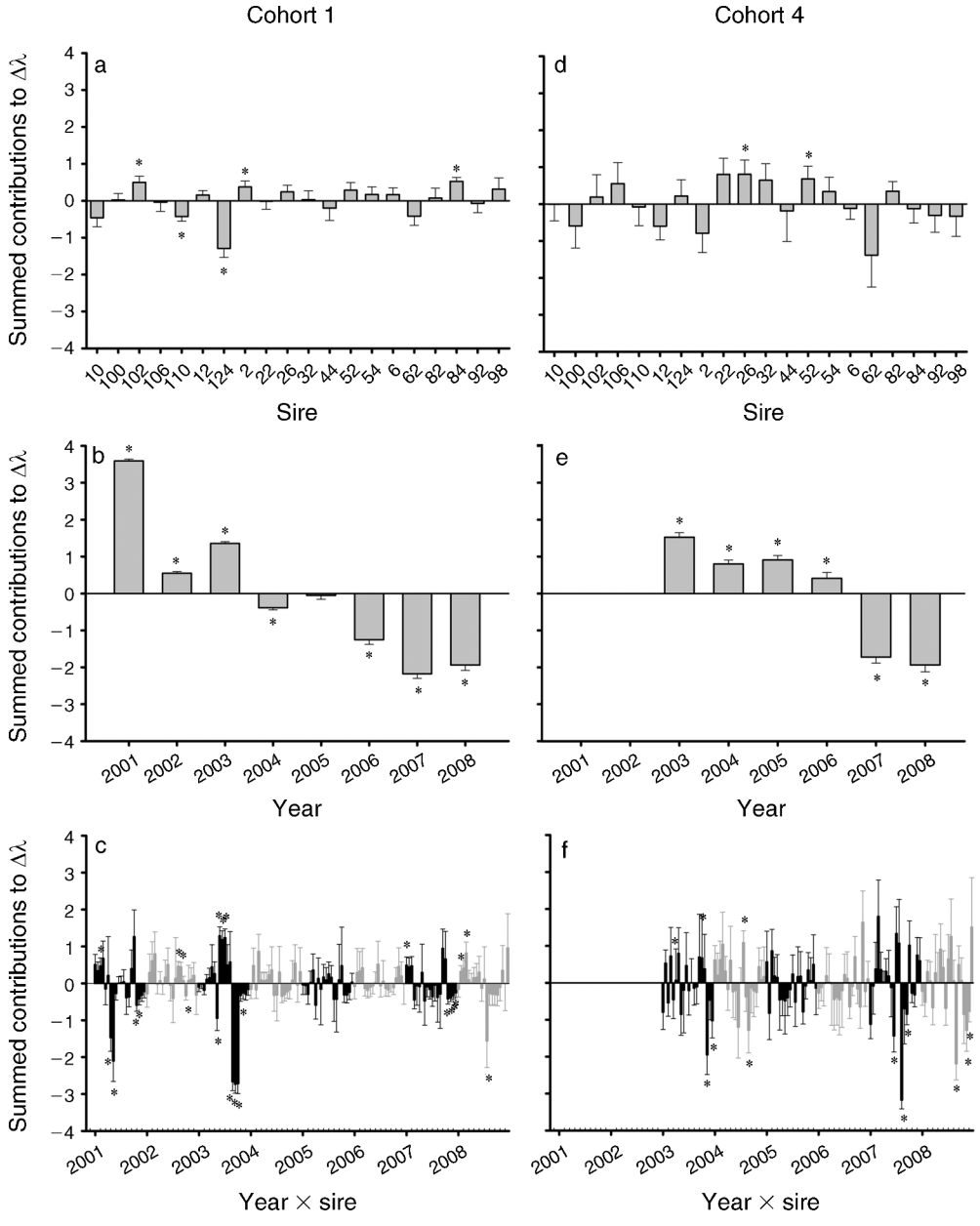

FIG. 1. Impact of genetic and temporal environmental variation on the population growth rates (λ) of two cohorts of *Plantago lanceolata* at Shadwell, Virginia, USA, assessed via life table response experiment (LTRE) analysis. Magnitudes of LTRE contributions to Δλ in (a–c) cohort 1 and (d–f) cohort 4 are shown. Factors tested include (a, d) sire, (b, e) year, and (c, f) year × sire. Error bars and asterisks denote standard errors and significance ($P < 0.05$), respectively.

expression of demographic traits indicates that demographic patterns may vary in ways not predicted via analyses of environmental impacts alone. Adaptively, demographic plasticity may serve plants in ways similar to behavioral plasticity in animals given that plants do not move and thus their "behavior" is limited to changing size and shape, which may mitigate the demographic impact of a changing environment (Gross et al. 2010). The long-term demographic impacts of early-life conditions and growth autocorrelations are little explored and may further alter any additive effects of genes and environment on demography (Pfister and Wang 2005, Nussey et al. 2006).

While studies evaluating the impacts of individual variation and stochasticity in the demography of wild populations are common (e.g., Pfister 1998, Pfister and Stevens 2003), such studies of the impacts of genetic variation are rare. The link between genetics and demography is typically approached from the other way around, by assessing the impact of past demo-

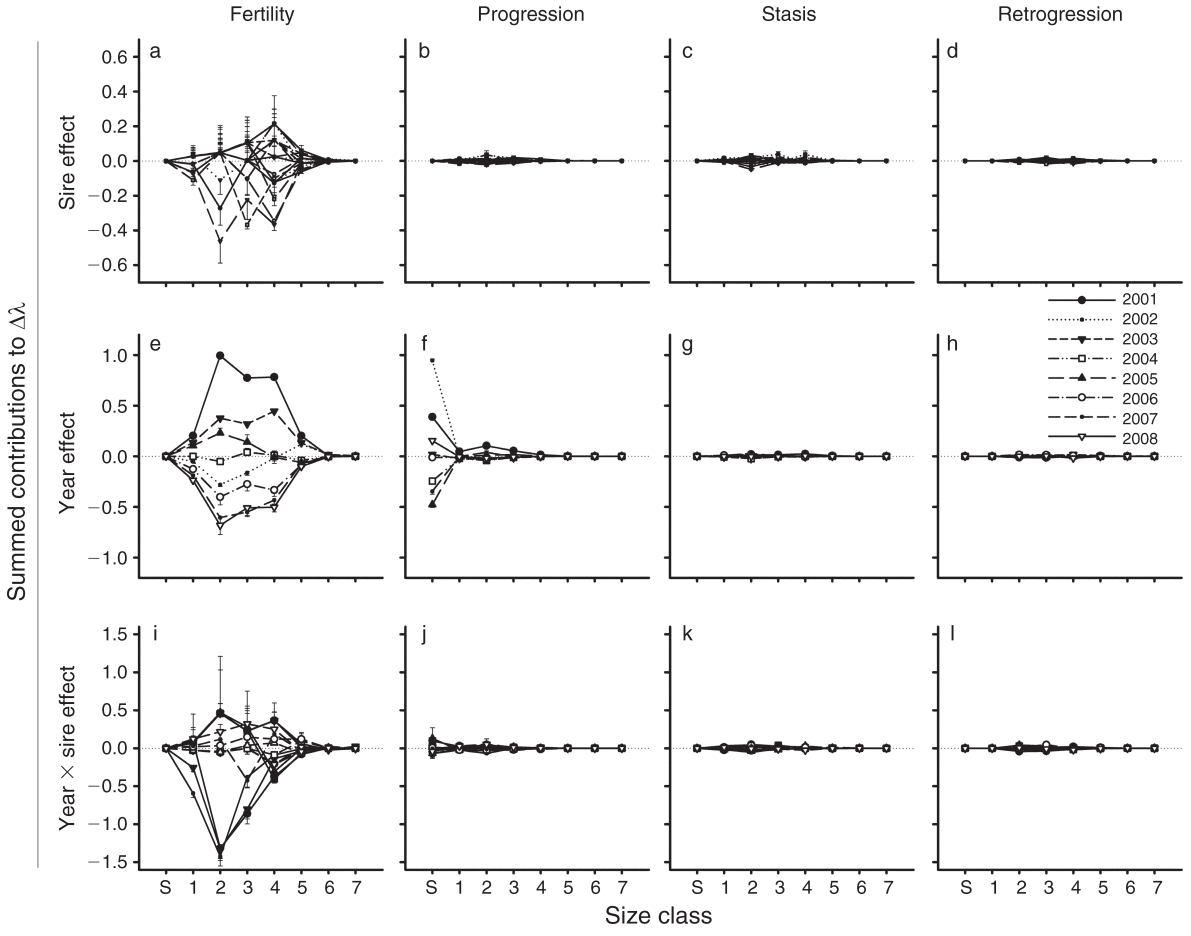

FIG. 2. Impact of genetic variation in demographic transition types on λ in cohort 1: LTRE decomposition of summed contributions to Δλ by size class in cohort 1. Shown are effects of (a–d) sires, (e–h) years, and (i–l) year × sire on λ through fertility, progression, stasis, and retrogression transitions, respectively. The *x*-axis represents size class, with seedlings (S), followed by tiny (1), small (2), small-medium (3), medium (4), medium-large (5), large (6), and giant (7) adults. Size was determined by leaf number, with classes defined in *Methods: Population projection modeling*. Sire effects (a–d) include all 20 sires, simply to show that sires differ. Year × sire effects (i–l) are illustrated with sires 124 and 2 only. Effects for sire 124 are denoted with solid symbols and solid lines, while effects for sire 2 are denoted with open symbols and dashed lines. Error bars denote standard errors.

graphic and evolutionary events on current genetic variation (e.g., Nagata et al. 1998, Goodman et al. 2001, Glinka et al. 2003). However, evolutionary response to natural selection is determined by the available genetic variation in a population. In *Plantago*, the impact of particular sires varied across years and cohorts, suggesting that the impact of any particular genotype changes with changing environmental conditions. This genotype-by-environment interaction is likely to maintain genetic variance over time in the population (Thompson 1991).

Evolution via natural selection is an important component of population dynamics, even in perennial, size-based systems such as *Plantago* (Barfield et al. 2011). Natural selection should lead to different genetic composition over time, and demographic patterns, even the associated stable distributions, should reflect this shift. Our simulation analysis in particular suggested that, under the assumption of a temporally stochastic environment, fitness and population growth rate may differ from expectation as genotypes less able to handle environmental variability become a smaller and smaller part of the population. Indeed, the shifting of genotypes over time likely changes population dynamics to reflect changed frequencies of genotypes, which likely all have different mortality and reproduction patterns. The eventual dominant genotypes can be difficult to predict, as they varied by cohort in this study and likely change according to the influences of variable norms of reaction. Fit within the framework developed by Hairston et al. (2005), in which rates of change in traits are decomposed into evolutionary vs. ecological components, we suggest that the evolutionary component of the change in growth rate over time is at least biologically significant, and possibly as significant as the ecological component.

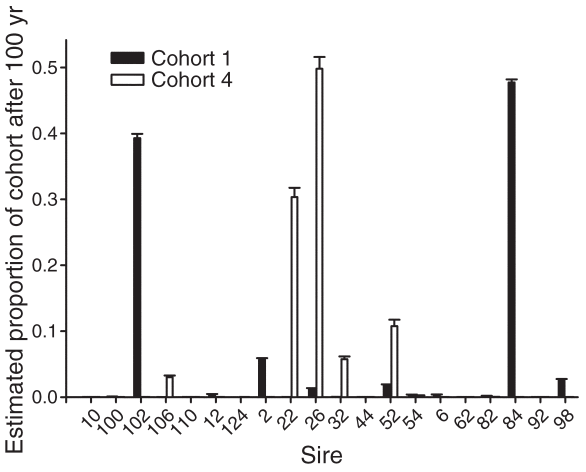

FIG. 3. The genetic compositions of cohorts 1 and 4 after 100 years projected via stochastic simulation. Bars indicate the proportion of each cohort from each paternal lineage (+SE), with the same succession of environments used for both cohorts.

Wild populations may evolve quite rapidly due to strong natural selection in the wild. Measured rates of evolution via natural selection vary from slow to quick, with recent analyses showing profound evolutionary change within a few generations, even in morphological traits (Reznick et al. 1997, Hairston et al. 2005). The evolutionary response to natural selection is contingent on appreciable additive genetic variance existing in the population under selection. Although demographers and population ecologists often suggest the importance of particular traits to fitness via perturbation analyses (de Kroon et al. 1986, Benton and Grant 1999, Sæther and Bakke 2000), we are currently unaware of studies that estimate the portion of the variability in these traits due to genetic variance. In this study, sires varied in their impact on λ via fertility, and we argue that such genetic variation may be important for population projections.

Age did not appear to exert a strong influence over demographic rates in this study. Although the first year of life exerted a strong influence on λ in all LTRE analyses, other years were as strong and sometimes stronger. Population growth rate and fitness are often sensitive to early-life stages and conditions in short-lived species (Kalisz and McPeek 1992, Franco and Silvertown 2004). Conditions and life history traits during the juvenile stage often exert strong impacts on later life stages, extending all the way to rates of senescence (Lindström and Kokko 2002, Nussey et al. 2007). In another analysis of this data set, growth in the first year had a negative impact on life span in the cohort that experienced the greatest growth early on, while it had a positive or no impact on the other cohorts (Shefferson and Roach 2010). However, environmentally induced cohort effects may have obscured age-related patterns in LTRE effects. Although cohort effects were not significant in the GLM analysis, we note that significant LTRE deviations did occur in the four-cohort analysis (Appendix E).

We make three suggestions for demographic analysis. First, there is a genetic basis to demographic traits that should be explored (Metcalf and Pavard 2007). Because such links are often not made in studies, the actual impact of management strategies on population growth rate via changes to particular component demographic processes is not known. Second, population growth rate in most if not all wild populations is likely to be influenced by interactions between environmental and intrinsic influences that may lead to unpredictable changes in population dynamics. In this study, each cohort exhibited its own unique demographic behavior, even though all cohorts were genetically equivalent initially and planted randomly in the same site. Third, we advocate further research on the impacts of phenotypic plasticity and natural selection on long-term demography. Demographic rates here were strongly plastic in the short term, and it is unclear what impacts this can have beyond the study period. On the one hand, this may result in a buffering of demographic trends over the long term, particularly if large amounts of genetic variation are preserved. On the other hand, plasticity may cause strong deviations from previous patterns, particularly if populations are small or more genetically homogenous. Further, natural selection should remove those genotypes least able to handle environmental stress and stochasticity over the long term, suggesting that demographic patterns should change over long periods simply due to the impact of differing genetic compositions. The development of further long-term field-based studies with strict breeding designs will help tease such intricacies out.

Intrinsic sources of demographic variation can have dramatic influences on the evolutionary trajectory of a population and its population viability (Beissinger et al. 2008). The environment interacts with intrinsic sources via altered expression and the restructuring of the genetic composition of populations. Plants in particular are known to encounter high levels of temporal environmental variation in their population vital rates (Doak et al. 2002), and our results suggest that genetic and cohort-based variation are also important. Better integration of population genetic data, which is already used to assess conservation risk, and a greater focus on in situ cohort experimentation with breeding may provide the means to tease apart the influences of these factors and present reliable predictions of population trajectories.

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Supplemental Material

Appendix A

Distributions of adult size classes across years for different paternal lineages in cohort 1 (*Ecological Archives* E093-070-A1).

Appendix B

Details of vital rate estimation, matrix construction, and LTRE analysis (*Ecological Archives* E093-070-A2).

Appendix C

Exploration of fertility assumptions and their impacts on λ (*Ecological Archives* E093-070-A3).

Appendix D

Estimates of projected population growth rate (*Ecological Archives* E093-070-A4).

Appendix E

LTRE analysis of four-cohort data set (*Ecological Archives* E093-070-A5).

Appendix F

Decomposition of LTRE conributions to $\Delta\lambda$ in cohort 4 (*Ecological Archives* E093-070-A6).