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Asynchrony in individual and subpopulation fecundity stabilizes reproductive output of an alpine plant population

Ellen Waddle,[1,5] Lucas R. Piedrahita,[2] Elijah S. Hall,[3] Grace Kendziorski,[1] William F. Morris,[4] Megan L. DeMarche,[1] and Daniel F. Doak[1]

[1]*Environmental Studies Program, University of Colorado, Boulder, Colorado 80302 USA*
[2]*Biology Department, Appalachian State University, Boone, North Carolina 28608 USA*
[3]*Biology Department, Juniata College, Huntingdon, Pennsylvania 16652 USA*
[4]*Department of Biology, Duke University, Durham, North Carolina 27708 USA*

Abstract. Population-wide outcomes such as abundance, reproductive output, or mean survival can be stabilized by non-synchronous variation in the performance of individuals or subpopulations. Such "portfolio effects" have been increasingly documented at the scale of subpopulations and are thought to play an important role in generating stability of population phenomena in the face of environmental variation. However, few studies quantify the strength and origin of portfolio effects at the finer scale of individuals. We used 16 yr of fruit production and climate data for an alpine plant to dissect the scale of portfolio effects in reproduction, as well as the contribution of individual traits including size and flowering time in driving reproductive output. Asynchrony in reproductive success substantially reduces variation in population-level reproductive output, with approximately one-fourth of this stabilizing effect arising from individual differences, mostly not those characterized by measured traits, and approximately three-fourths from asynchrony across subpopulations. These results emphasize the different scales and causes of portfolio effects. The decomposition for portfolio effects we provide can facilitate similar breakdowns of the strength and causes of these effects in other systems.

Key words: climate; environmental variation; intraspecific trait variation; portfolio effect; Silene acaulis; synchrony.

Introduction

What mechanisms stabilize ecological systems, from populations to ecosystems, has been an enduring question. While fluctuating environmental conditions will tend to drive variation in community or population attributes, asynchrony in the responses of sub-components of these systems (e.g., individuals within a population or differing species within a community) can dampen variability in aggregate attributes to be below that expected if all components varied in synchrony. These so-called portfolio effects initially entered the ecological literature in efforts to understand community stability due to asynchrony among species (Doak et al. 1998, de Mazancourt et al. 2013), but have since been evaluated for subunits within populations of single species to determine how their differing dynamics can contribute to stability of population-wide attributes (Anderson et al. 2013, Schindler et al. 2015). For example, if subpopulations respond differently to common environmental fluctuations, overall variance can be less than expected based on common responses across all parts of the population. The magnitude of such asynchronies can result in substantial portfolio effects in many systems, with asynchrony across species or subpopulations contributing to aggregate population stability and altered ecosystem functioning (Schindler et al. 2010, Thorson et al. 2014, Abbott et al. 2017, Hui et al. 2017, Yamane et al. 2017; Dibner et al., *in press*). These effects have been quantified for a suite of community and population attributes, including community biomass (Leps 2004), population numbers (Schindler et al. 2015), thermal tolerance

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diversity in fish (Anderson et al. 2015), community productivity, and nutrient retention (Tilman 1996).

However, by focusing largely on asynchrony between subpopulations, but not between individuals, analyses of population-level portfolio effects have not been able to examine how trait differences may drive differential environmental responses or add stability to populations. Individuals within a population can differ in ecologically important ways, including multiple intrinsic (e.g., life history strategy, age) and extrinsic (e.g., microclimate and community interactions) features, all of which could generate asynchrony in performance that could in turn result in portfolio effects. Standard demographic analyses capture many of the most obvious differences among individuals due to age, size, or life stage (Caswell 2001); because many populations typically include individuals spanning a range of life stages at any given point in time, differences in their environmental responses can act to reduce population fluctuations (Schindler et al. 2010, Moore et al. 2014). However, more cryptic genetic, phenotypic, or microsite variation can also lead to quite different life history trajectories among individuals, with potential effects on population outcomes (Acker et al. 2014, Vindenes and Langangen 2015). For example, individual variation in growth rates has been shown to alter both the variance and mean of population growth (Bjornstad and Hansen 1994, Pfister and Stevens 2003, Kendall et al. 2011, Jansen et al. 2012). In addition to stable differences in performance, individuals can also vary in their responses to climate or other demographic drivers (Anderson et al. 2015, Abbott et al. 2017), with this diversity potentially dampening population-level variability in the face of fluctuating climate or other drivers of performance.

Here, we examine the contributions of individual trait variation and disparate climate responses to the stability of population-wide reproductive output for an alpine plant species. We link 2 yr of intensive monitoring of individual flowering time differences with a 17-yr data set on annual reproductive success of *Silene acaulis,* a long-lived alpine cushion plant (henceforth, *Silene*). The individual-level data span four subpopulations and include information on plant size and sex as well as flowering time. These data allow us to distinguish between portfolio effects generated by individual differences and by subpopulation effects. Individual traits range from fully intrinsic (e.g., sex) to a complex mix of intrinsic and extrinsic (e.g., flowering time, which is likely to be strongly influenced by microtopography). We focus our analyses on three questions: (1) How does individual sex, size, and flowering time influence fruit production? (2) How do these individual traits interact with annual climate variation to create synchrony or asynchrony in individual performance across time? (3) Does asynchrony generate meaningful portfolio effects for this population, and at what scale do these effects occur? In particular, is the majority of the stabilizing effect seen within or

between subpopulations, and how much is due to obvious trait differences vs. unexplained variation? While deterministic population growth is not highly sensitive to mean reproductive output for *Silene*, reproduction is the most variable vital rate across time and the elasticity of stochastic growth rate to reproductive variability is comparable to that of other vital rates (Morris and Doak 2005). In addition, at its southern range limits reproduction and establishment are limiting steps in the life cycle of this long-lived species (Doak and Morris 2010), such that decreased variability in reproductive output is likely to confer stability in shifting climatic conditions.

METHODS

Long term demographic data

We studied permanently marked and mapped individual *Silene acaulis* (Caryophyllaceae) at four subpopulations on Niwot Ridge, Colorado (Appendix S1: Fig. S1). Subpopulations differ in elevation (3,540–3,613 m above sea level), slope, aspect, and microhabitat, ranging from sparsely vegetated fell fields (sites SN1 and SN2) to more densely vegetated dry meadows (sites SN3 and SN4). Permanent plots were initially mapped in 2001 and have since been visited annually to record the size and fruit production of each plant. We quantify plant size each year as the two-dimensional area of the plant's living tissue (Doak and Morris 2010). As a proxy for seed production, we count the number of mature, seed-producing fruits produced by each plant in each year. An average of seven to nine seeds are produced per fruit (Shykoff 1988).

Phenology and sex of plants

In 2016 and 2017, we collected flowering data for a randomly selected subset (13–24%) of the plants at each of the four study sites (see Appendix S1: *Supplemental Methods* for more detail). The number of open flowers on each plant was counted every 2–5 d during the flowering season. These data were used to estimate initial flowering day, date with highest number of flowers, total days that flowers were open, total flower count, and fruit set (total fruit count/total flower count). We use mean first flower date across 2016 and 2017 as our measure of individual flowering phenology, as preliminary analyses showed that it was a much stronger predictor of fruit set than were our other measures of flowering phenology. First flower date for an individual was strongly correlated across the 2 yr (Spearman rank correlation $r = 0.847$, Appendix S1: Fig. S2). We also recorded the sex of each flowering plant. *Silene* in the Rocky Mountains are gynodioecious, consisting of females (which produce seeds) and hermaphrodites (which produce both pollen and seeds). Sex is most likely genetically determined in *Silene* (Delph et al. 1999).

Climate data

We used interpolated climate summaries (PRISM Climate Group 2004) to obtain consistent climate estimates across the 17-yr span of the study. Based on previous analyses of *Silene* performance (Doak and Morris 2010, DeMarche et al. 2018), we used total precipitation during the growing period from June through August, and mean July temperature, indicative of overall summer temperature, as our two climate summaries. These two variables are not strongly correlated (Appendix S1: Table S1). There were no multi-year climate extremes (i.e., drought) during the study period (Appendix S1: Figs. S3 and S4).

Data analysis

For our analyses, we used only plants initially marked in 2001 that survived through 2017, bore a fruit in at least one year, and flowered in both 2016 and 2017; 27% of the population never bore fruit, 35% did not flower in either 2016 or 2017, (though only 3% flowered in one but not the other year), and 8% of initially marked plants that were ever reproductive died over the course of the study. These restrictions resulted in a total sample of 183 individuals. Preliminary analyses showed no evidence for an across-year cost of reproduction that would drive fluctuations in individual reproductive effort (Appendix S1: *Supplemental Methods*).

Given the ubiquitous concern about overdispersion in count data, we used generalized mixed negative binomial models with a log-link to predict annual fruit number per plant within each subpopulation as a function of three fixed plant traits (plant size, sex, and mean date of first flower), six annual fixed climate variables (precipitation and temperature in the prior and current years, as well as squared effects of precipitation and temperature), and a random effect of individual to account for repeated measures (which almost entirely eliminated overdispersion in our data). We included interactions between trait and climate variables, allowing for possible two-way and three-way interactions. We also fit models for individuals in all subpopulations, with subpopulation included as a predictor variable. See Appendix S1: *Supplemental Methods* for rules used in model set construction. Models were fit using the glmer.nb function in the lme4 package (Bates et al. 2015), with model support judged by the Akaike information criterion corrected for sample size (AIC_c). We standardized all numerical predictors to compare effect sizes on fruit production. All analyses were conducted in R version 3.5.1 (R Core Team 2018).

We next used the outputs of these models to investigate the cause of potential portfolio effects. In particular, we used a variance decomposition approach to ask how strongly asynchrony contributed to a portfolio effect, or the reduction of variation in total fruit production below that predicted if all plants were perfectly correlated in their reproductive fluctuations through time (cf. Loreau

and de Mazancourt 2008), and what factors most contributed to these effects. We first examined the portfolio effect within each subpopulation separately. To distinguish the contributions to the portfolio effect of explainable trait variation, including interactions with climate, vs. unexplained variation, we partitioned each plant's annual fruit production, F, into the model predicted value, M, and the residual value, R. For each time t and plant i, $F_{it} = M_{it} + R_{it}$, while the subpopulation-wide fruit production, F_i is just the sum of these individual-level sums. Standard variance relationships then show that the variance of F_i can be expressed as a sum of the variances and covariances of the M_i and R_i terms. We divide these terms into several categories useful in understanding the contribution of different effects to the temporal variance in subpopulation fruit production:

$$
\begin{aligned}
\mathrm{Var}\left(\sum_i F_i\right) = {} & \sum_i \mathrm{Var}(M_i) + \sum_i \mathrm{Var}(R_i) \\
& + \sum_i \sum_{j \neq i} \mathrm{Cov}(M_i, M_j) + \sum_i \sum_{j \neq i} \mathrm{Cov}(R_i, R_j) \\
& + \sum_i \sum_{j \neq i} \mathrm{Cov}(M_i, R_j)
\end{aligned} \quad (1)
$$

For simplicity of presentation, below we refer to sums on the right-hand side of this equation as Svar(M_i), Svar(R_i), Scov(M_i, M_j), Scov(R_i, R_j), and Scov(M_i, R_j), where i and j index plant individuals. Note that M_i and R_i, arising from general linear models, have approximately zero covariance. We compare the empirical components of the covariance sums in this decomposition with their theoretical maxima, which would occur if all correlations were one, such that each covariance term would be equal to the product of the two variables' standard deviations. To quantify the contribution of each covariance term to the reduction of total variance, we use the difference between the theoretical maximum covariance and the actual summed covariance, divided by the maximum aggregate variance. For example, the contribution of cov($M_i M_j$) is $\left(\sum \mathrm{Cov}(M_i M_j)_{\mathrm{MAX}} - \sum \mathrm{Cov}(M_j M_j)_{\mathrm{OBS}}\right)/\mathrm{Var}(\sum F_i)_{\mathrm{MAX}}$. These contributions of different covariance terms sum to give the total proportional reduction in aggregate variance due to portfolio effects, with higher values indicating more reduction in variance. Since we are assuming that the observed variances of F_i and M_i values are fixed, the summed variance terms in Eq. 1 do not contribute to the overall portfolio effect. To facilitate comparison with past studies, we also report the synchrony index, ϕ, the ratio of observed aggregate variance to maximum aggregate variance (Loreau and de Mazancourt 2008). While we would ideally statistically test the significance of the portfolio effects seen, we expect predominantly positive, not uncorrelated, variation in the responses of individuals of the same species and thus compare observed values to those in which this variance

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is perfectly positively correlated, precluding any obvious use of randomization tests to ascertain significance.

We derived a similar decomposition for the variance in total fruit production across all four subpopulations. This decomposition takes the form

$$
\begin{aligned}
\mathrm{Var}\left(\sum_{k=1}^{4}\left(\sum_{i} F_i\right)\right) = \sum_{k=1}^{4}&\left(\sum_{i}\mathrm{Var}(M_{ik}) + \sum_{i}\mathrm{Var}(R_{ik})\right.\\
&+ \sum_{i}\sum_{j\neq i}\mathrm{Cov}(M_{ik}M_{jk}) + \sum_{i}\sum_{j\neq i}\mathrm{Cov}(R_{ik}R_{jk})\\
&\left.+ \sum_{i}\sum_{j\neq i}\mathrm{Cov}(M_{ik}R_{jk})\right)\\
+ \sum_{k=1}^{4}\sum_{l\neq k}&\left[\sum_{i}\sum_{j\neq i}\mathrm{Cov}(M_{ik}M_{jl}) + \sum_{i}\sum_{j\neq i}\mathrm{Cov}(R_{ik}R_{jl})\right.\\
&\left.+ \sum_{i}\sum_{j\neq i}\mathrm{Cov}(M_{ik}R_{jl})\right]
\end{aligned}
\tag{2}
$$

where k and l index subpopulation and i and j index plant individuals. In parallel with the decomposition used for separate subpopulations, we isolated summed terms for the variance and covariance of modeled and residual fruit production within each subpopulation (e.g., $\mathrm{Svar}(M_i)_1$, $\mathrm{Svar}(R_i)_1$, $\mathrm{Scov}(M_i, M_j)_1$, $\mathrm{Scov}(R_i, R_j)_1$, and $\mathrm{Scov}(M_i, R_j)_1$ for subpopulation 1) as well as the summed covariances between modeled values for plants in different subpopulations ($\mathrm{Scov}(M_i, M_j)_{k,l}$, where k and l indicate that plant i and j come from subpopulations k and l, respectively), between the residual values in different subpopulations ($\mathrm{Scov}(R_i, R_j)_{k,l}$), and between residual and modeled values for plants in different subpopulations ($\mathrm{Scov}(R_i, M_j)_{k,l}$). In making this decomposition, we use the sample of observed plants at each site, which ranges from 63 to 27. While it is possible to adjust the samples to give equal weight to each site, accounting for this unequal sample size, the results are not substantively changed, and we do not know the proportion of the entire regional population that is most similar in habitat to each of the four subpopulations.

Results

To visualize the variation in individual fruit production over time for each plant i, we plotted log(annual fruits$_i$/mean fruits$_i$), adding one to each annual value to deal with zeros. While these deviations in annual fruit production show substantial synchrony within subpopulations (Fig. 1A), there is also considerable variation among plants and across subpopulations; in particular, extreme years for fruit production differed substantially among subpopulations (Appendix S1: Fig. S5). Notably, early vs. late flowering individuals seem to show somewhat different patterns of fruiting, with early flowering plants appearing more synchronized than later flowering individuals (Fig. 1A), and all plants more variable and asynchronous in unexplained residual fruit production than predicted fruits (Fig. 1B, C).

The best-supported model for fruit production shows several large climate, trait, and subpopulation effects as well as substantial interactions between subpopulation and individual traits and climate (Fig. 2A, Appendix S1: Table S2). Fruit production increases strongly with plant size and earlier flowering across all sites, and female plants have higher fruit production in half of the subpopulations. Climate effects interact strongly with subpopulation, while the strongest individual interactions with climate variables are with plant sex and area. The model estimates of fruit production show fairly synchronized predictions within each subpopulation (Fig. 1B), and variation in estimated fruiting was similar but not identical across the subpopulations (Appendix S1: Table S3). Support for the top model was similar to that of the next several alternative models, which all included similar terms and magnitudes of coefficients (Appendix S1: Table S2); $\Delta \mathrm{AIC_c}$ for the second-best model was 0.31, and the only difference between the top models was the inclusion/exclusion of sex and area by temperature interactions. Most effects were also similar across subpopulations (Fig. 2A, Appendix S1: Tables S4–S7). Because multiple models with each model set had relatively high AICc weights, we report weighted (from $\mathrm{AIC_c}$ weights) means and SDs for decomposition results across all models with $\mathrm{AIC_c}$ weight >0.01 (Appendix S1: Table S3). Tri-gamma pseudo-r^2 values for GLMMs were calculated for the best models using the r.squaredGLMM function from MuMIn (Barton 2018). The best model has a conditional r^2 of 0.443 and marginal r^2 of 0.271, which is comparable to the r^2 values for the four separate subpopulation models (Appendix S1: Table S8).

Residual values after accounting for the model predictions show substantial variation (Fig. 1C), and some of this variation is highly correlated across plants within subpopulations. For example, 2008 was a year of unexplained low fruit production by many plants at SN1 and SN2, while 2014 showed very low production for many plants in SN2, 3, and 4. These patterns in residuals imply that some common environmental factors that are not captured by our annual climate data may account for shared responses. It is likely that some differences among the subpopulations occur due to idiosyncratic snow deposition effects; SN1 and SN2 are more wind exposed and see little spring snow accumulation, while both SN3 and SN4 can accumulate snow during spring storms in ways that would be hard to predict from our climate variables, potentially driving correlated residual deviations in fruit production.

All four subpopulations show substantial portfolio effects, with synchrony index (ϕ) values (actual/maximum theoretical variance) much less than one: 0.036, 0.105, 0.126, and 0.391 for SN1–SN4, respectively. The majority of these effects are due to the low covariances between residual values and between modeled and
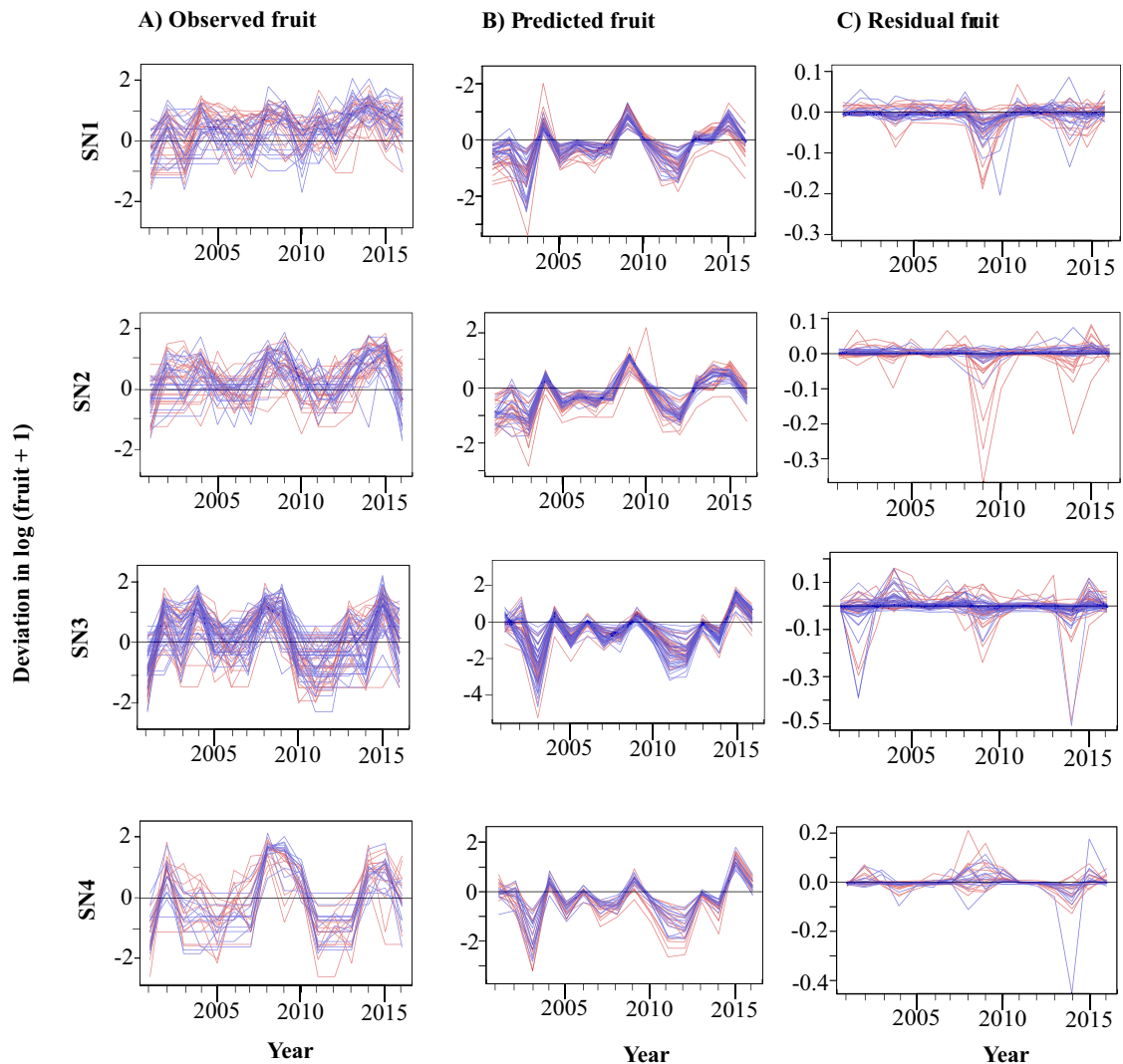
Fig. 1. Individual deviations in actual, predicted, and residual fruit production in each subpopulation (SN1 to SN4). Data are annual log deviations, calculated as log((annual value +1)/(mean value +1)) for (A) observed fruits for each individual plant over time, (B) annual predicted fruits from a best-supported model (Appendix S1: Table S2), and (C) annual residual values from this model. Blue lines indicate plants that flower earlier than average and red lines indicate plants that flower later than average. Horizontal lines indicate mean fruit number.

residual values (Fig. 2B; Appendix S1: Fig. S6 and Table S3). In contrast, there are high positive covariances in modeled values at all sites, dampening total portfolio effects (recall that negative or weak covariance is the origin of portfolio effects). Thus, the majority of the portfolio effect within each subpopulation is due to unexplained differences in individual reproductive output, rather than differences in annual performance that can be attributed to the traits we quantified and their interactions with measured climate variation.
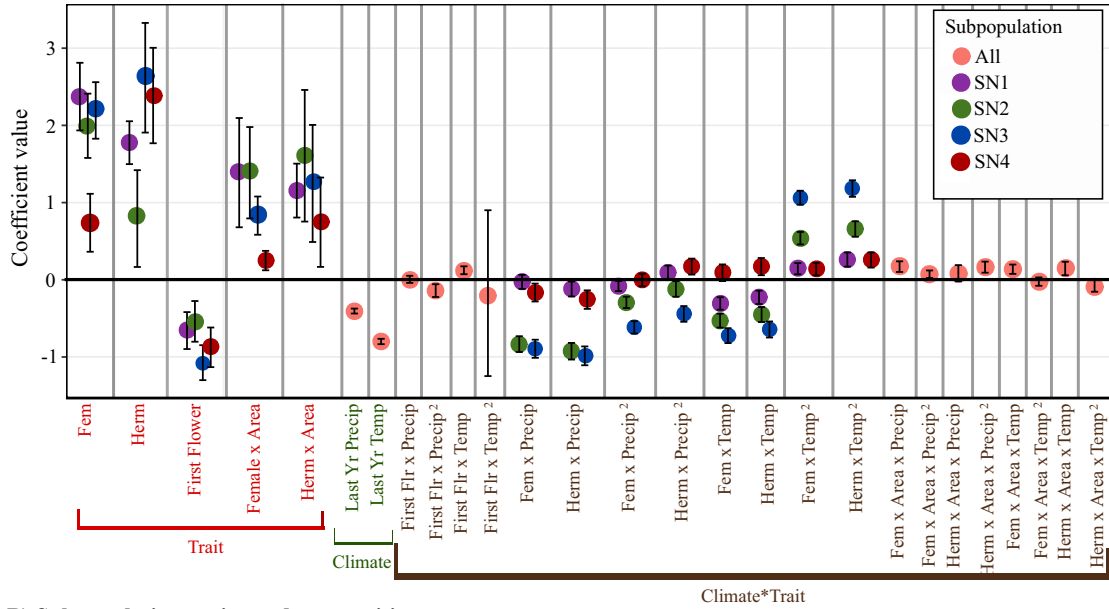
The variance decomposition across all subpopulations combined shows that total variance is reduced by 90% from a theoretical maximum, and that within-subpopulation covariance terms generally had smaller

contributions to generating portfolio effects than were covariances between subpopulations (Fig. 2C). Summed across categories of covariance terms (Fig. 2C), the overall effect of covariance between subpopulations contributes 77% of the total reduction. Unlike the within-subpopulation effects, we also see that across subpopulations the model-estimated values show considerable asynchrony and thus contribute significantly to the total portfolio effect (Fig. 2C).
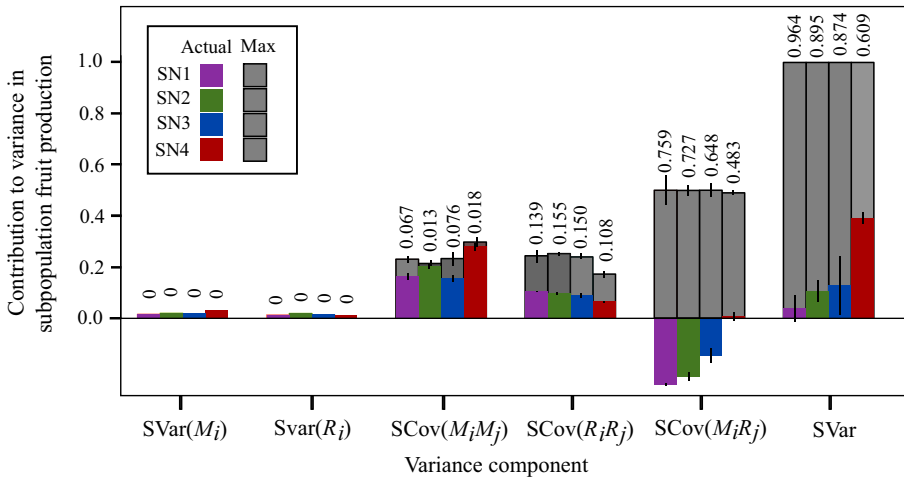
DISCUSSION

Asynchrony between subpopulations across a range of scales can act to stabilize population-level
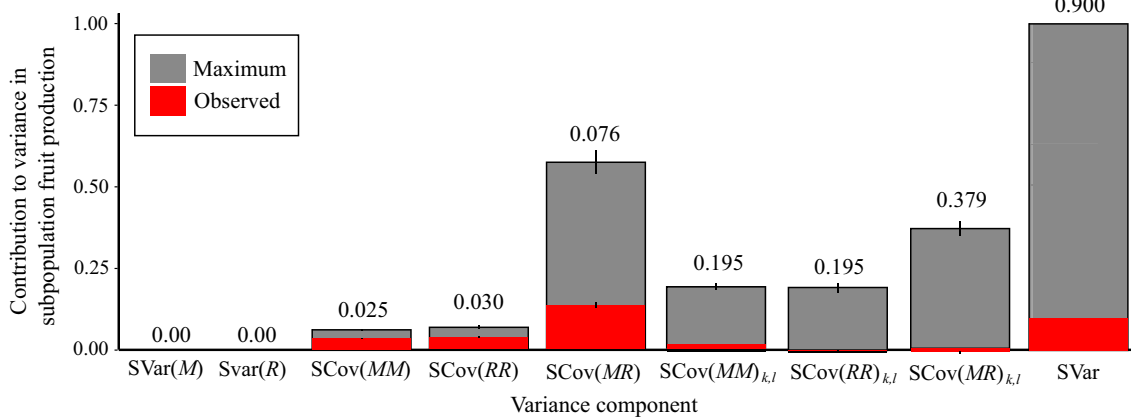
FIG. 2. (A) Standardized coefficients (±SE) for the best-supported model of fruit production across all subpopulations (Appendix S1: Table S2). Colors indicate different categories of effects. (B) Contributions to portfolio effects within each

(Fig. 2. *Continued*)

subpopulation. For each component, colored bars show actual values and are superimposed onto maximum possible values, shown in gray. For each subpopulation, all variance component values are rescaled so that total maximum variance equals one. The contribution of each component to the overall proportional reduction in variance due to the portfolio effect is shown above each bar, with the value over the total bar (Svar) showing the total reduction in variance. Results are shown from the best-supported model for each subpopulation, with error bars showing weighted standard deviations from all top models with >0.01 AIC weight (Akaike information criterion). See Appendix S1: Table S3 for subpopulation model averaged results. See *Methods* for description of the variance components. (C) Contributions to portfolio effects across all subpopulations. $\text{Scov}(M, M)_{k,l}$, $\text{Scov}(R, R)_{k,l}$, and $\text{Scov}(M, R)_{k,l}$ indicate between subpopulation covariance effects, while all other terms show individual-level (within-subpopulation) covariances. Error bars show AIC_c weighted (AIC corrected for sample size) standard deviations for coefficients across all models >0.01 AIC_c weight, reflecting model uncertainty.

phenomenon, such as total biomass, reproduction, or abundance, by reducing aggregate variation. Most analyses of these population portfolio effects have been conducted only at the level of large subunits of populations. Our work extends this by comparing the relative roles that individuals and subpopulations play in stabilizing population-level responses. Additionally, we offer a novel way to break down components of variance to better pinpoint the origin of portfolio effects. We find the largest contribution to overall stability of a key population attribute, reproductive output, arises from asynchrony between plants in different subpopulations, but also show that individual asynchrony within subpopulations accounts for a substantial fraction, 23%, of the total portfolio effect we observe. This implies that future research on stabilization of population performance should consider not just obvious differences between subpopulations, such as different habitats or life history strategies, but also less obvious asynchronies that occur between individuals within the same population segment.

We also find important differences in the roles of trait-linked vs. residual variation in reproduction in generating portfolio effects. Although our modeling framework allowed for multiple interactions between individual traits and climate variables, we found that within subpopulations, trait-linked estimates of reproductive variation across time were highly correlated and thus contributed little to portfolio effects. In contrast, asynchronous residual variation in individual fruit production had far larger contributions to the stability of subpopulation reproduction. Across subpopulations, we found that both trait-linked and residual asynchronies contributed strongly to portfolio effects, although residual covariance was still the most important in stabilizing population-level reproduction.

The strong effects of unexplained variation imply that important differences between individuals in performance may not always be easy to attribute to habitat, spatial proximity, or easy-to-observe traits, and thus that care should be taken to consider the importance of unmeasured heterogeneity at the level of individuals. The genesis of these effects could be genetic differences, biotic interactions (e.g., local density of competing plants), other microsite effects (e.g., microclimate or soil), or even contributions from simple demographic stochasticity. While testing which of these factors actually contribute the most to individual-level variation may be nearly impossible in many field studies, the overall importance of this unexplained variation is likely to be robust across systems.

Here, we focus on a single attribute of individuals and populations, total reproductive output, to dissect patterns in portfolio effects. This univariate output is convenient because it is measureable for individuals and populations, is not binary at the individual level (as, for example, is survival), and is more variable between individuals for slow-growing species like *Silene*, than is, for example, growth. Furthermore, reproductive output is often strongly influenced by traits such as size or phenology for which individual-level data are commonly available. In addition, past work has shown that variation in reproduction has nontrivial effects on stochastic growth rates of *Silene* populations (Morris and Doak 2005). Moreover, temporal stability in reproductive output (seed production) is likely to be important for population stability in the face of shifting climate conditions (Greene et al. 2010). Nonetheless, more synthetic measures of the population, such as growth rates, total numbers, or biomass, are more often the fodder of population analyses, including those of portfolio effects. We expect that for these measures, a breakdown of portfolio effects would reveal similar importance of unexplained individual variation, as cryptic individual variation likely affects multiple aspects of individual performance (Fox and Kendall 2002, Pfister and Peacor 2003). Although the methods we use to decompose variance will need to be modified to deal with response variables like individual fitness and population growth, which depend on multiple aspects of performance, the same general approach can be adapted to judge the importance of different effects for aggregate stability.

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