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1980, Boyce et al. 2006). Consider that population size grows from time t to t +

Once having estimated vital rate correlations, we then elucidate their role in stochastic population dynamics. The contributions of vital rates to stochastic population dynamics are typically unequal, because vital rates differ in both year-to-year variability (Pfister 1998) and sensitivity (e.g., Franco and Silvertown 2004). As a result, the strength of a correlation is not necessarily predictive of its effect on population growth (Doak et al. 2005). We used stochastic simulations to quantify the individual effects of pairwise and [illegible] (volume and leaf area, respectively) but a discrete variable in .

temporal variances and covariances. In addition, the output of a Bayesian analysis is a posterior probability distribution for each parameter mean, variance, and covariance, reflecting the uncertainty in the estimates given the uncertainty in the data. These posterior distributions allow us to transfer the uncertainty in vital rate estimation to the uncertainty in the output of the population models.

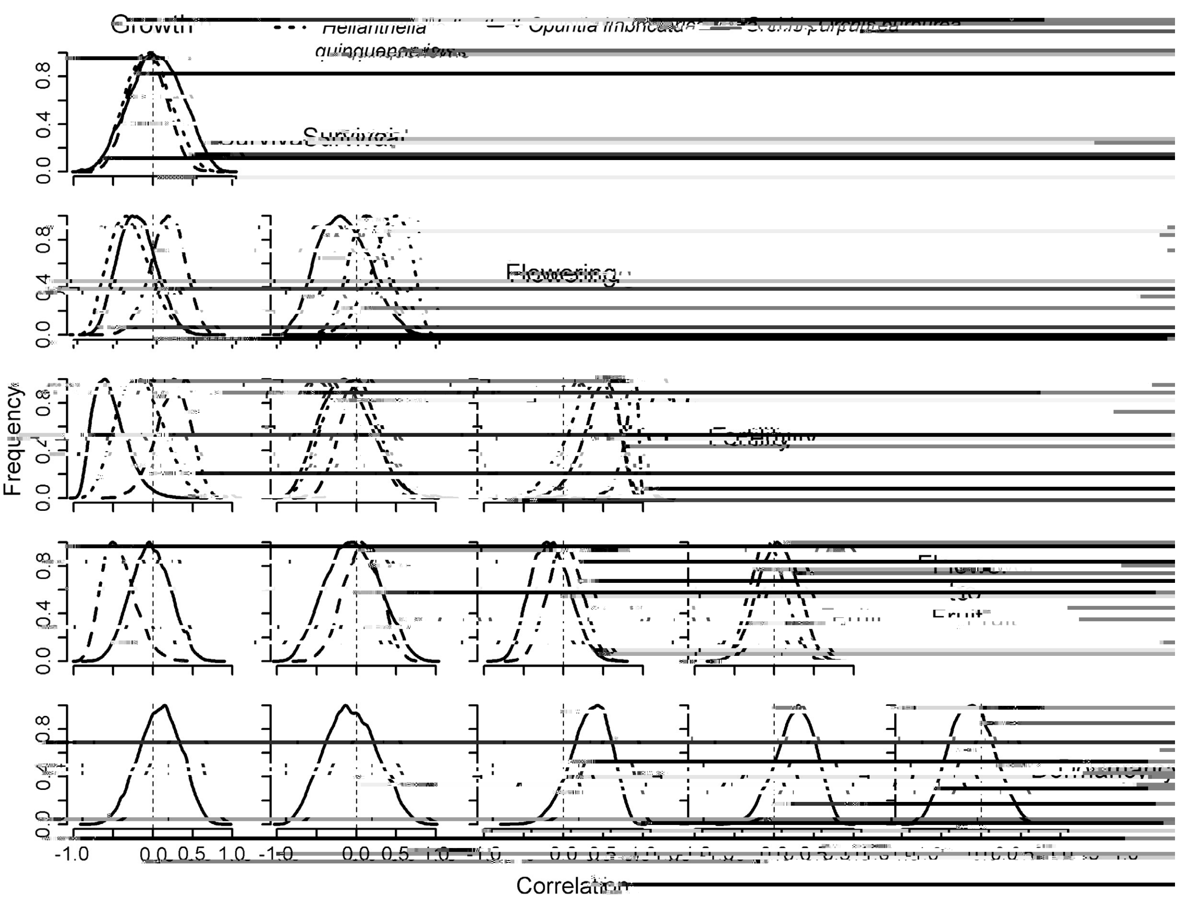
We fit our models in Stan (Stan Development Team 2015), a programming language that allows Bayesian inference without requiring conjugacy of priors. The central objective of our statistical models was to estimate the correlations and variances of vital rates (the lower-level parameters of) separately. In stochastic population dynamics, the variance of vital rates and the correlation among vital rates have distinct effects (Doak et al. 2005). In previous studies, ecologists have estimated using an inverse Wishart prior (e.g., Ibáñez et al. 2009). This is the only known conjugate prior for and is thus an obligate choice for the most popular packages that fit Bayesian models using Gibbs sampling (e.g., Lunn et al. 2000, Plummer 2003). However, using an inverse Wishart prior for produces biased estimates whereby correlations and variances are not independent (Gelman and Hill 2007). We therefore used Stan, which fits models using No-U-Turn (Hoffman and Gelman 2014) or Hamiltonian Monte Carlo (Duane et al. 1987) sampling, a powerful alternative that allowed us to estimate variances and correlations independently.

We fit the Bayesian models using uninformative priors for all parameters. We decomposed the variance–covariance matrix to = diag( ) diag( ), where diag() returns a diagonal matrix, **P** is a matrix of pairwise correlation coefficients, and is a vector that contains the standard deviations. We estimated the correlation matrix g/T1 using distribution. We first simulated population dynamics using the mean values of vital rate parameters' joint posterior. To quantify uncertainty in our inferences for $Var(\lambda_i)$ and λ_S, we replicated simulations by running 100 separate population projection models built using 100 random samples from the joint posterior distribution of all vital rate parameters, including those associated with from the joint posterior distribution of the vital rate parameters. The distributions of Δλ values therefore reflect all of the uncertainty in our estimates of vital rate coefficients, including uncertainty in estimates of temporal variances and correlations.

[illegible]

(1) [illegible]

Vital rate correlations varied greatly in both sign and magnitude, and uncertainty in their estimates was high (Fig. 1). Across all species and vital rates, there were only two correlations for which the posterior probability distribution indicated an unambiguous sign (their 95% credible interval excluded zero): the positive correlation between the probability of flowering and fertility in (mean ρ = 0.82; 95% CI = [0.51; 0.96]) and the negative correlation between growth and fertility in (mean ρ = -0.53; 95% CI = [−0.85; −0.05]). There were two additional correlations for which a majority of the posterior distribution indicated a consistent sign (but the 95% CI included zero): the positive correlation between the probability of flowering and fertility in (mean ρ = 0.45; 95% CI = [−0.06; 0.80]) and the negative correlation between growth and flower-to-fruit transition probability in (mean ρ = -0.43; 95% CI = [−0.77; 0.03]). For the cactus , there were no correlations for which the posterior distribution indicated a clear sign and most posterior modes were weak in magnitude. The positive correlations between flowering and fertility in and indicate that years in which flowering was more likely were also years of greater seed production by flowering plants; this correlation was also positive, on average, for , though there was greater uncertainty in its estimate (Fig. 1). On the other hand, the negative correlations indicate that years of greater reproductive effort or success were associated with smaller gains in size, and vice versa. In , the negative correlation occurred between growth and the number of flowers produced, regardless of whether the flowers set fruit. In , the negative correlation occurred between growth and floral abortion (high floral abortion [i.e., low flower-to-fruit transition]



. 1. Posterior probability distributions of vital rate correlations. Each panel represents a vital rate pair. Line types represent species.

was associated with high growth, and vice versa). The remaining correlations, which were most of the correlations, did not have a predominant sign within or across species, and their mean magnitude was usually small (Fig. 1).

that most vital rate correlations had little effect on Var(λ_i). Moreover, the strongest mean contribution to Var(λ_i

suggested that, for all three species, vital rate correlations should consistently buffer the variability of growth rates, on average (Appendix S5: Fig. S1). LTREs showed an average decrease in Var($\lambda_{1,i}$) for [illegible] (−8.59%), [illegible] (−4.26%), and [illegible] (−17.37%). However, just like the estimates from simulation experiments, the uncertainty associated with the LTRE estimates was large: posterior probabilities were distributed across positive and negative effects of correlations, and credible intervals included zero (Appendix S5: Fig. S1).

(4) [illegible]?

Across all three species, the effect of vital rate correlations on long-term stochastic population growth rate (λ_s) was small in magnitude and virtually zero, on average (Fig. 4B). The credible intervals of λ_s show very small effects that range from −0.49% to +0.88% in [illegible], from −0.01% to +0.03% in [illegible], and from −0.25% to 0.25% in [illegible]. On average, vital rate correlations changed the stochastic population growth rate by +0.17% in [illegible], +0.002% in [illegible], and −0.01% in [illegible].

Posterior distributions for the absolute values of λ_s are shown in Appendix S6. Results indicated that the [illegible] population is almost certainly declining, because no posterior sample produced λ_s values greater than 1.0 (95% CI = [0.93; 0.99]). [illegible] is also projected to decline, though the uncertainty in its stochastic population growth rate included the possibility of positive growth (95% CI = [0.91; 1.04]). On the other hand, the posterior distribution of λ_s in [illegible] exceeded 1.0, so this population is expected to grow (95% CI = [1.05; 1.10]). All of these predictions for population viability were insensitive to whether demographic correlations were on or off (Appendix S6). Thus, qualitatively and even quantitatively, explicit accounting of vital rate correlations did not change our understanding of the dynamics and viability of these populations.

[illegible]

Natural populations encounter stochastic fluctuations in demographic vital rates from year to year. Theory predicts a potentially important role for correlated vital rate fluctuations in long-term population viability broadly representative, the non-trivial task of quantiautocorrelation on stochastic population growth of primates, effects comparable in magnitude to our results from perennial plants, to low baseline demographic variability. We speculate that vital rate correlations may generally have negligible effects for populations already buffered against temporal variability, as long-lived organisms tend to be (Morris et al. 2008).

Another surprising result from our simulations was the direction of correlation effects on year-to-year variability (Fig. 4A) relative to the direction of effects on λ_s (Fig. 4B). While none of these effects were strong, the mean increase of Var(λ_i) in [illegible] and [illegible] was not associated with a mean decrease in λ_s, as would be predicted by classic theory. We speculate that this result may have been caused by the canonical link functions that we used to model temporal variability in vital rates (e.g., Eqs. 2b, 3b, 4b). These link functions are standard tools for the development of stochastic IPMs (Rees and Ellner 2009) but they introduce some nonlinear averaging. Canonical link functions implicitly assume that demographic processes respond nonlinearly to random variation. As a consequence, nonlinear averaging might arise whereby the value of a vital rate in an average year is greater or less than the value of the vital rate averaged across years. The magnitude of this difference depends on the magnitude of year-to-year variability and on the concavity of the link function (Ruel and Ayres 1999). For instance, the log-link function we used in our fertility models (Eq. 4b) is concave up. As a result, an increase in temporal variation could potentially increase average fertility and, potentially, stochastic population growth rate (Barraquand and Yoccoz 2013). A deeper analysis of this issue falls outside the scope of our study, but we suggest that it warrants greater attention in the methodological literature on stochastic demography. Given the small magnitudes of the effects we detected (Fig. 4B) any contributions of nonlinear averaging in our study are unlikely to affect our qualitative conclusions.

Our λ_s results suggest that vital rate correlations should have negligible evolutionary implications in our three species. Vital rate correlations are expected to modulate rates, strong correlation between these two processes may importantly affect population dynamics in a variable environment. These hypotheses regarding the role of life cycle complexity are well suited to theoretical study, which we suggest would be a fruitful area for further work.

Conclusion

In this study, we show that temporal vital rate correlations in three perennial plant species are usually weak but occasionally strong, and in both directions. While vital rate correlations have potential to modify year-to-year variability and thus stochastic population growth, we found that correlations had virtually no effect on stochastic population dynamics and did not modify our inferences of population viability. Explanations for the negligible effects of vital rate correlations may include the predominance of weak correlations, low sensitivities and low variability of the few vital rates that were strongly correlated, and fluctuations in size structure over-riding fluctuations in vital rates. Our results offer potentially good news for population ecologists, because the process of estimating and modeling vital rate correlations is data-intensive and computationally nontrivial.

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