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Using statistics to design and estimate vital rates in matrix population models for a perennial herb

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Abstract

Matrix population models are widely used to assess population status and to inform management decisions. Despite existing theories for building such models, model construction is often partially based on expert opinion. So far, model structure has received relatively little attention, although it may affect estimates of population dynamics. Here, we assessed the consequences of two published matrix structures (a 4×4 matrix based on expert opinion and a 10×10 matrix based on statistical modeling) for estimates of vital rates and stochastic population dynamics of the long-lived herb *Astragalus scaphoides*. We explored the ways in which choice of model structure alters the accuracy (i.e., mean) and precision (i.e., variance) of predicted population dynamics. We found that model structure had a negligible effect on the accuracy and precision of vital rates and stochastic stage distribution. However, the 10×10 matrix produced lower estimates of stochastic population growth rates than the 4×4 matrix, and more accurately predicted the observed trends in population abundance for three out of four study populations. Moreover, estimates of realized variation in population growth rate due to fluctuations in population stage structure over time were occasionally sensitive to matrix structure, suggesting differential roles of transient dynamics. Our study indicates that statistical modeling for choosing categories in matrix models might be preferable over expert opinion to accurately predict population trends and can provide a more objective way for model construction when the biological knowledge of the species is limited.

KEYWORDS

demography, matrix population model, plant population dynamics, stochasticity, vital rates

1 | INTRODUCTION

Matrix population models are widely used to assess population status and to inform management decisions (e.g., Crone et al., 2011; Crouse, Crowder, & Caswell, 1987; Menges, 2000; Öst, Ramula, Lindén, Karell, & Kilpi, 2016; Ramula, Knight, Burns, & Buckley, 2008), as evidenced by the accumulation of hundreds of matrices for different species across taxa (Salguero-Gómez et al., 2015, 2016). In matrix models, individuals are assigned into discrete categories based on their age, size or life stages, and vital rates (the survival, growth, and fecundity of individuals) are then estimated separately for each category (Caswell, 2001). Model structure determines the amount of data per category in a

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matrix model, which may affect estimates of vital rates and, consequently, estimates of population growth rate (Fiske, Bruna, & Bolker, 2008). For a given data set, a smaller matrix consists of more individuals per category than a larger matrix, and therefore, might result in more precise estimates of vital rates, given that vital rates within each category are homogeneous enough (Moloney, 1986; Vandermeer, 1978). However, not all vital rates are necessarily affected by matrix structure. As an example, vital rates that fluctuate little over time (e.g., adult survival in long-lived organisms) might be estimated reliably based on a small number of individuals (Fiske et al., 2008).

While model structure may be relatively unimportant in some cases, it can be important in others. For example, matrix structure may have a minor effect on the long-term population growth rate (e.g., Picard & Liang, 2014; Tenhumberg, Tyre, & Rebarber, 2009) but a substantial effect on short-term transient dynamics (Tenhumberg et al., 2009). Transient dynamics is important in changing environments and can play a major role particularly in reintroduced or invasive populations that may not have reached their stable stage structure (Ezard et al., 2010; Iles, Salguero-Gómez, Adler, & Koons, 2016; Stott, Townley, & Hodgson, 2011). A related phenomenon affects ordinary stochastic population dynamics: realized variation in growth rate depends on both variation in vital rates and variation in stage structure over time (Ellis & Crone, 2013). Therefore, if we extrapolate from extreme cases of transient dynamics, we would predict that variation in stage structure is more important for larger matrices than for smaller matrices. A previous comparative study of stochastic population dynamics across different plant species found that the relative contribution of variation in stage structure to realized variation in population growth rate increased with increasing matrix dimension, while the relative contribution of variation in vital rates decreased with increasing matrix dimension (McDonald, Stott, Townley, & Hodgson, 2016). If matrix structure is critical to the conclusions of sources for variability of population growth rate, this may affect our interpretation of population dynamics, and consequently, our conclusions on how to effectively manage populations.

Ideally, individuals in the adjacent categories of matrix models exhibit different vital rates. Despite the fact that theories exist for how to choose categories for structured population models (Merow et al., 2014; Moloney, 1986; Salguero-Gómez & Plotkin, 2010; Vandermeer, 1978), model structure is usually at least partially based on expert opinion on relevant categories, for matrix models in particular. As a consequence, model structure varies among species and sometimes even among populations of the same species (e.g., Brys, Jacquemyn, Endels, de Blust, & Hermy, 2005; Lehtilä, Syrjänen, Leimu, Begoña Garcia, & Ehrlén, 2006) by either reflecting study aims, the biology and life history of a given species (e.g., seed bank, dormant stages, semelparity, iteroparity), and/or the amount of demographic data available. For example, in published matrix population models of plant and animal species, dimension varies from two categories up to more than 20 categories (mean = 4 categories for plants; Salguero-Gómez et al., 2015, 2016), with matrix dimension generally increasing with the amount of data for perennial plants (Ramula, Rees, & Buckley, 2009). We should mention here that matrix structure does not only refer to matrix dimension, but it also refers to biological assumptions underlying the model. A matrix model can be constructed in different ways depending on, for example, how vital rates are assumed to change when individuals senesce (Tuomi et al., 2013) or undergo periods of prolonged dormancy (Jäkäläniemi, Crone, Närhi, & Tuomi, 2011).

An alternative to expert opinion for choosing categories in matrix population models is statistical modeling, in which the variability of vital rates is explored a priori between alternative categories. For instance, Jäkäläniemi et al. (2011) used generalized linear mixed models (GLMMs) to test whether vital rates for the perennial orchid, *Epipactis atrorubens*, differed among dormant individuals with different demographic history, and consequently, to inform whether a single category or multiple dormant categories were necessary to be included in a matrix population model. As the statistical modeling is likely to be a more objective way for choosing categories than expert opinion, it might more accurately predict the long-term population growth rate. However, this modeling approach is less frequently used in practice (but see e.g., Jäkäläniemi et al., 2011, Gremer, Crone, & Lesica, 2012, Alahuhta et al., 2017), and we are not aware of studies that have compared estimates of stochastic population dynamics between matrix models based on expert opinion and statistical modeling.

Here, we used two published matrix structures to evaluate dynamics of the long-lived perennial herb, *A. scaphoides*, and to compare the ways in which choice of matrix structure alters predicted population dynamics. For this species, Lesica (1995) published a 4×4 matrix that was constructed based on expert opinion (i.e., stage classes were defined according to biological relevance), and Gremer et al. (2012) later published a 10×10 matrix for which stage classes were chosen based on statistical modeling. For both matrix structures, we estimated annual vital rates with GLMMs rather than used observed data because this elegant but underused technique reduces sampling variation (Altwegg, Schaubb, & Roulin, 2007; Morris et al., 2011; Williams & Crone, 2006). More specifically, we compared both the accuracy and precision of estimates of vital rates (fit with GLMMs), stochastic population growth rate and stochastic stage distribution. We also compared the

contributions of variability of vital rates and stage structure to realized variation in growth rate. We predicted that (a) estimates of binary vital rates would be more precise in the smaller matrix due to more individuals per stage category, while the larger matrix based on statistical modeling would more accurately predict observed trends in population abundance due to its finer biological resolution; (b) the overall estimates of average stochastic population growth rate and stochastic stage distribution would be similar regardless of matrix structure (i.e., point estimates would be similar and their confidence intervals would overlap); and (c) the two components of realized variation in population growth rates—changes in vital rates and stage structure over time—would depend on matrix structure, with the former being smaller and the latter being larger in the 10×10 matrix than in the 4×4 matrix. In other words, changes in vital rates would decrease, while changes in stage structure would increase with increasing matrix dimension.

2 | MATERIALS AND METHODS

2.1 | Study species and demographic data

A. scaphoides (Fabaceae) is an iteroparous, perennial herb with an estimated life span of 21 years (Ehrlén & Lehtilä, 2002). It inhabits sagebrush steppe in Montana and Idaho, and flowers with yellow inflorescences in May–June. Median age to first reproduction is 3 years (Lesica, 1995), after which high flower and seed production tend to occur in alternate years (Crone, 2013; Crone & Lesica, 2004; Lesica, 1995), resulting in considerable fluctuations in vital rates over time (Gremer et al., 2012). The species exhibits prolonged dormancy (i.e., nonseed stages stay belowground for one or more years before re-emerging) with most dormancy events only lasting 1 year (Gremer et al., 2012; Lesica, 1995).

Demographic data were collected from four populations of *A. scaphoides*; Sheep Corral Gulch (N45 06 21 latitude, W113 02 44 longitude) and Reservoir Creek (N45 08 26, W113 10 24) in Montana, and McDevitt Creek (N44 55 23, W113 43 42) and Haynes Creek (N45 00 19, W113 42 06) in Idaho by annually monitoring the fates (vegetative, flowering, dormant) of plants in established transects (see Lesica, 1995 for details). Plants with unbranched stems were divided into those with more or less than six leaves (leaf counts were not recorded), and the number of seed pods was counted for flowering plants. The minimum and maximum pairwise distances between the study populations were about 10 and 50 km, respectively. The surveys were initiated in different years, but we used demographic data from the overlapping period 2003–2014 (12 years and 11 transition matrices for each population) to enable comparisons among populations. Final datasets contained on average 117 ($\pm SD$ = 65.5) monitored individuals per year (see Table S1 in Supporting Information for annual sample sizes).

To examine the effect of matrix structure on estimates of population parameters, we constructed 4×4 and 10×10 matrices based on the two previously published population models. The 4×4 matrix, based on expert opinion, is structurally identical to that previously used by Lesica (1995) and Tenhumberg, Crone, Ramula, and Tyre (2018) for this species, and consists of small vegetative plants (<6 leaves), large vegetative plants (≥6 leaves), flowering plants, and dormant plants. In this matrix, individuals from any stage category can enter the dormant category and vice versa (Figure 1a, Table S2 in Supporting Information). The 10×10 matrix is based on statistical modeling and, consequently, differences in vital rates between adjacent stage categories (Gremer et al., 2012). This matrix mirrors the matrix

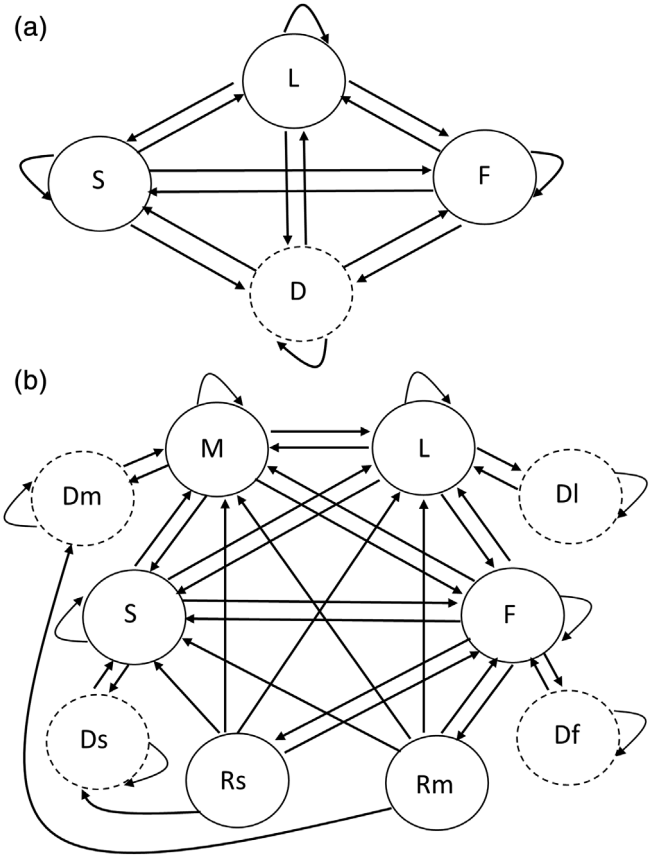


FIGURE 1 Life cycle graphs of the perennial herb *Astragalus scaphoides* resulting in (a) a 4×4 matrix based on expert opinion and (b) a 10×10 matrix based on statistical modeling. The arrows indicate transitions between different life stages: small recruits (Rs), medium recruits (Rm), small vegetative plants (S), medium vegetative plants (M), large vegetative plants (L), flowering plants (F) and dormant plants (D*x*) reflecting different aboveground stages *x* before dormancy. Dormant stages are circled with a dotted line

used by Gremer et al. (2012) for Sheep Corral Gulch population except that it does not contain a short-term seed bank because no evidence for seed dormancy was found in a statistical analysis across all four study populations (Table S3 in Supporting Information). The stage classes in the 10 × 10 matrix are: small recruits (newly emerged plants with <6 leaves), medium recruits (newly emerged plants with 6 or more leaves including flowering plants), small vegetative plants (<6 leaves), medium vegetative plants (6 or more leaves), large vegetative plants (evidence of aboveground branching), flowering plants, small dormants (defined as in Gremer et al., 2012 based on the state before dormancy), medium dormants, large dormants and flowering dormants (Figure 1b). Therefore, the larger matrix contains multiple dormant categories and individuals from a given nondormant stage category can enter a corresponding dormant category only and vice versa (Figure 1b, Table S2). Moreover, the 10 × 10 matrix distinguishes new recruits from older vegetative plants that have emerged earlier, while they are pooled with vegetative stages in the 4 × 4 matrix (Figure 1, Table S2).

For each matrix structure, we estimated vital rates using GLMMs to account for sampling variation that can bias annual estimates (Appendix S1 in Supporting Information). Although some studies have used GLMMs to estimate vital rates (e.g., Altwegg et al., 2007; Gremer et al., 2012; Jäkäläniemi, Ramula, & Tuomi, 2013; Morris et al., 2011; Tye, Dahlgren, Øien, Moen, & Sletvold, 2018; Williams & Crone, 2006), this approach is still poorly known among demographers. Following Morris and Doak (2002), we analyzed stage transitions as conditional vital rates (i.e., survival, flowering probability conditioned on survival, dormancy conditioned on survival and not flowering, and growth conditioned on survival and not flowering or not being dormant; see Tables S2, S4 in Supporting Information). We used binomial family, logit link GLMMs to estimate conditional vital rates (function "glmer" in the *lme4* package in R 3.5.1; R Development Core Team, 2018). Annual offspring production was estimated with a Poisson family, log link GLMM using the number of recruits at year $t + 1$ as a response variable and the log-number of flowering plants +1 at year t as an offset (1 was added to enable analyses for years when no flowering plants were observed). All statistical models included an intercept only with year as a random effect to produce annual estimates of vital rates after correcting for varying sample size. If annual estimates of vital rates were not possible to calculate due to missing data for a given year, we used the model intercept, that is, the maximum likelihood estimate of the average on a link scale. Using year as a random effect in statistical models for individual vital rates reduces sampling variation resulted from different sample sizes over the study period (Altwegg et al., 2007; Morris et al., 2011; Williams & Crone, 2006), making this estimation method preferable to the traditional way of constructing matrix models that directly utilizes observed transitions without attempts to control for sampling variation.

2.2 | Accuracy and precision of vital rates

To compare the accuracy and precision of vital rates between the two matrix structures, we calculated the mean and standard error of back-transformed binary vital rates (survival, flowering probability conditioned on surviving, dormancy conditioned on surviving and the probability of transitioning to large plants conditioned on surviving, 12 vital rates in total; Figure 2) using the "delta method" function in the *msm* package of R (Jackson, 2011). This function (based on a Markov multistate model fit by maximum likelihood) enabled us to calculate the standard error of the weighted mean of vital rates for the larger 10 × 10 matrix according to the vital rates from the smaller 4 × 4 matrix. Note that the survival and flowering probability of flowering plants, as well as the survival of dormant individuals are identical in both matrix structures and were not considered (Figure 1). Similarly, the fecundity transitions were excluded from this comparison as our a priori prediction did not hold for them (sample sizes are smaller in the smaller matrix than in the larger matrix, and the main fecundity transition from flowering plants to small plants is identical in both matrix structures). We then examined differences in the means and standard errors of these 12 binary vital rates between the two matrices. As the means represented different types of vital rates, we first tested differences in the point estimates between the two structures separately for each vital rate using a t test (based on their means and associated errors). To summarize the outcomes of these multiple individual tests, we used an empirical adaptation of Brown's method (function "empiricalBrownsMethod" in the *EmpiricalBrownsMethod* R package; Poole, 2018), which is an extension of Fisher's method and tests overall differences among dependent comparisons in each population (Poole, Gibbs, Shmulevich, Bernard, & Knijnengburg, 2016). For the standard errors, we tested a directed hypothesis (i.e., estimates from the smaller matrix would be more precise) with a paired t test in R. The paired t test was used to consider the dependence of the vital rates estimated from the two matrix structures. We ran again comparisons separately for each population.

2.3 | Stochastic population dynamics and realized variation in growth rate

To explore estimates of population parameters resulting from the two matrix structures for each population, we used a matrix selection method. The selection of matrices is a

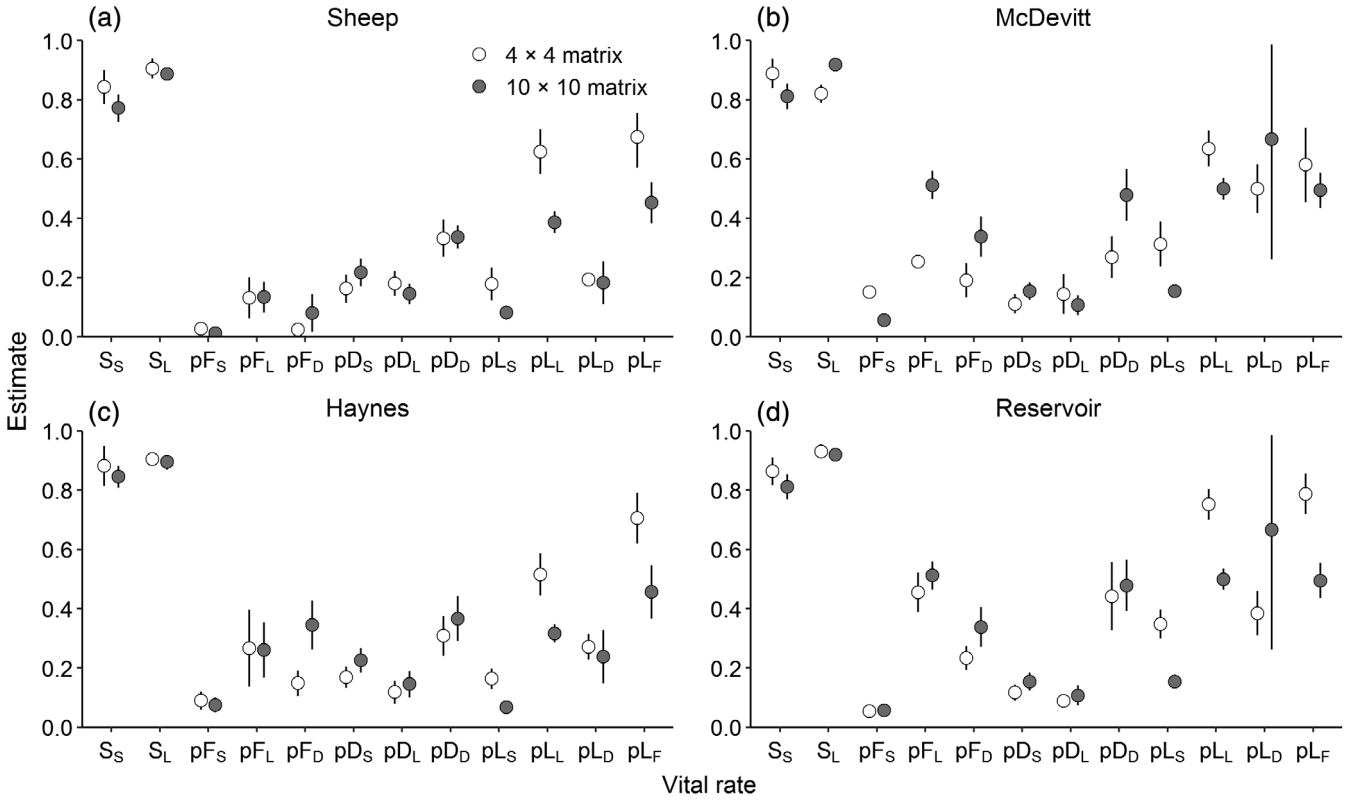


FIGURE 2 Accuracy (mean) and precision (±*SE*) of binary vital rates estimated using two matrix structures for four populations of the perennial herb *Astragalus scaphoides* (a–d). To enable comparison of vital rates, weighted means based on the delta method were used for the larger matrix (see Section 2 for details). Abbreviations for the conditional vital rates considered are: survival of small (s_S) and large plants (s_L); flowering probability of small (pF_S), large (pF_L), and dormant plants (pF_D); dormancy conditioned on surviving of small (pD_S), large (pD_L), and dormant (pD_D) plants; probability of transitioning to large plants from small (L_S), large (L_L), dormant (L_D) and flowering (L_F) plants conditioned on surviving

commonly used approach that maintains observed covariances among vital rates and typically includes between-year variation in them (Morris & Doak, 2002). To consider parameter uncertainty, we first sampled vital rates from a normal distribution based on their annual means (coefficients from GLMMs on logit and log scales for binary and fecundity rates, respectively) and standard errors (for annual estimates, extracted from GLMMs), and constructed a new set of 11 transition matrices per population (see Appendix S1 in Supporting Information for details). In cases where there were no data for a given vital rate in a given year, we used the ML coefficient and standard deviation estimated across years. All vital rates were back-transformed for the matrix models. We then simulated density-independent stochastic dynamics for 500 years with 1,000 replicates by randomly selecting a matrix from a set of new matrices ($n = 11$ per matrix structure) based on equal probabilities. This procedure was repeated 100 times, with each simulation consisting of a new set of vital rates per 1,000 replicates. All simulations were started from the same number of individuals that were equally distributed among different matrix stages. Stochastic population growth rate (log λ_s) was calculated based on the logarithm of population sizes from two consecutive years over time, averaging them across 1,000 replicates and further across 100 simulations. The first 100 years were discarded to achieve stochastic steady state dynamics. Using a larger number of simulations or replicates had a minimal effect on model outputs (S. Ramula, unpublished). In addition to stochastic growth rate, we calculated average stochastic stage distribution from these simulations for each population. To enable comparison of stochastic stage distributions between the two matrix structures, we summed the stage distribution of the larger 10×10 matrix to correspond the structure of the smaller matrix: stages 1–2 represented small vegetative plants, stages 3–5 represented large vegetative plants and stages 7–10 represented dormant plants, while stage 6 (flowering plants) was identical in both matrix structures.

We assessed the accuracy of the stochastic population growth rates (estimated above) by comparing them to the growth rates calculated from population abundances during the study period, hereafter $r_{abundance}$ (Table S1). We calculated $r_{abundance}$ with a Poisson family, log-link GLMM using the number of plants during 2004–2014 as a response variable and the log-number of plants from the previous year (2003–2013) as an offset, year was included as a random intercept in the model.

To partition realized variation in growth rate of *A. scaphoides* into two different components (variation in vital rates and variation in stage structure over time), we followed the method and calculations described in Ellis and Crone (2013). This method separates the part of the observed annual population growth rate between two time-steps that is due to variation in vital rates (demographic variation) from the part that is due to fluctuations in population stage structure. For each population, we simulated stochastic density-independent dynamics as above and calculated the observed annual population growth rate (r_{obs}) between $t = 500$ and $t = 501$ as $\log(\Sigma(\mathbf{A}_{500}\mathbf{n}_{500})/\Sigma\mathbf{n}_{500})$, where $\mathbf{A}_{500}$ denotes the transition matrix and $\mathbf{n}_{500}$ denotes population stage structure from 500th time step. The component due to the difference in vital rates over time (r_{VR}) was calculated as the logarithm of the dominant eigenvalue of $\mathbf{A}_{500}$, and the component due to variation in stage structure (r_{SS}) was calculated as as $\log(\Sigma(\mathbf{A}_{500}/\lambda_{500}\mathbf{n}_{500})/\Sigma\mathbf{n}_{500})$. Note that r_{VR} and r_{SS} sum to r_{obs} (Ellis & Crone, 2013). To quantify dependencies, Pearson's correlation coefficients were then calculated between r_{obs} and r_{VR}, and between r_{obs} and r_{SS} (Ellis & Crone, 2013) across 100 simulations, with each simulation consisting of 1,000 replicates.

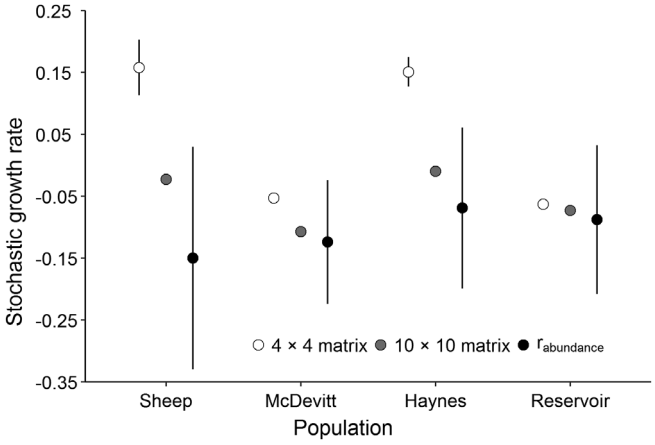


FIGURE 3 Stochastic population growth rates (mean ± 95% CI calculated across 100 simulations with each consisting of 1,000 replicates) resulting from two matrix structures (4 × 4 and 10 × 10) and growth rates calculated from observed population abundances ($r_{abundance}$) using a generalized linear mixed model for four populations of the perennial herb *Astragalus scaphoides* (a–d). Note that CIs are sometimes small and therefore invisible at the current scale

3 | RESULTS

3.1 | Accuracy and precision of vital rates

Comparison of the 4 × 4 and 10 × 10 matrices revealed that the accuracy (i.e., mean) of vital rates differed

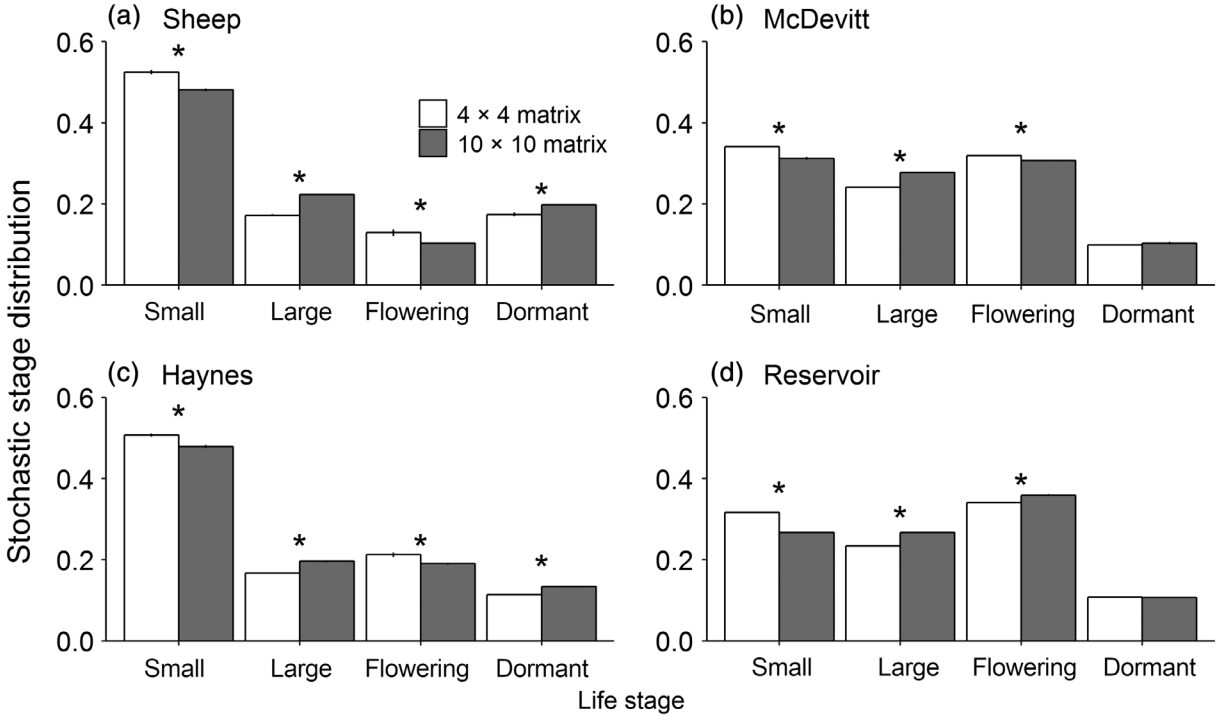


FIGURE 4 Observed stochastic stage distribution (mean ± 95% CI calculated across 100 simulations with each consisting of 1,000 replicates) resulting from two matrix structures (4 × 4 and 10 × 10) for four populations of the perennial herb *Astragalus scaphoides*. The stages of the larger matrix are summed to correspond to those of the smaller matrix (see Section 2 for details). Significant differences in the estimates between the two matrix structures (defined as nonoverlapping CIs) are indicated by asterisks. Note that CIs are sometimes small and therefore invisible at the current scale

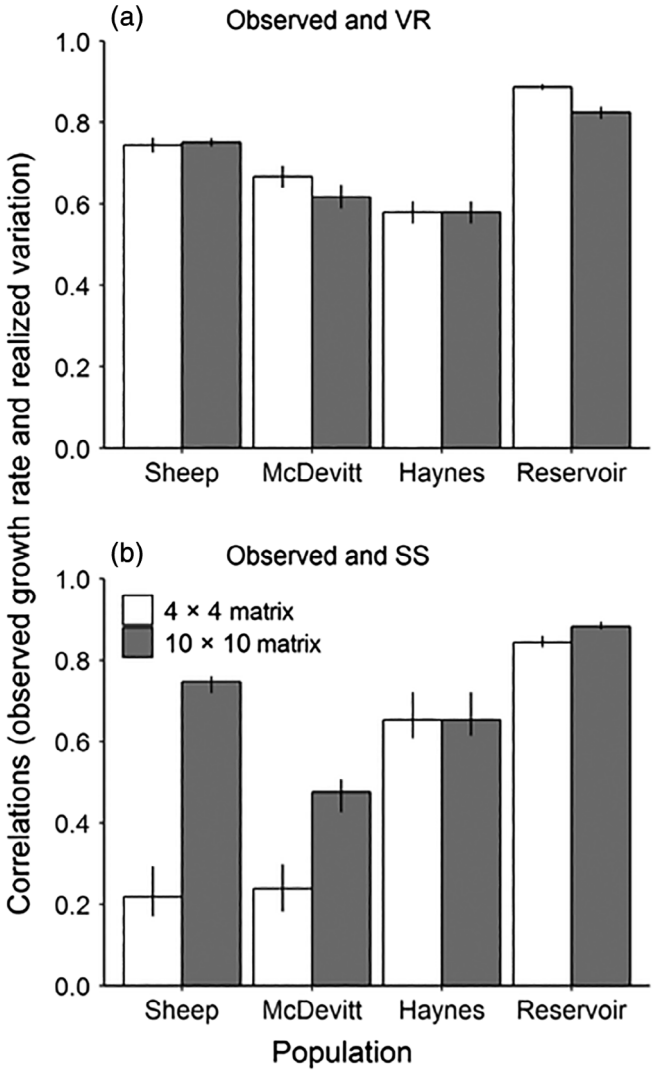


FIGURE 5 Pearson's correlation coefficients (mean ± 95% CI calculated across 100 simulations with each consisting of 1,000 replicates) between (a) observed growth rate and (b) components of realized variation in growth rate resulting from two matrix structures (4 × 4 and 10 × 10) for four population of the perennial herb *Astragalus scaphoides*. Abbreviations are: observed = observed growth rate between two consecutive time steps (r_{obs}), VR = realized variation in growth rate due to the variability of vital rates (r_{VR}) and SS = realized variation in growth rate due to the variability of population stage structure (r_{SS})

statistically significantly only in one (McDevitt Creek) out of four populations of *A. scaphoides* (Table S5 in Supporting Information). However, the differences in the vital rates were not systematic but depended on a vital rate in question (Figure 2b). The precision (i.e., standard error) of the vital rates did not differ between matrix structures in any of the four study populations ($p > .10$ for all paired t tests, $df = 11$, Table S5 in Supporting Information, Figure 2).

3.2 | Stochastic population dynamics and realized variation in growth rate

Matrix structure affected both the accuracy (mean) and precision (confidence intervals) of growth rate estimates in *A. scaphoides* (Figure 3). The larger matrix produced lower estimates of stochastic population growth rate than the smaller matrix in three out of four populations (Sheep Corral Gulch, McDevittt Creek, Haynes Creek; Figure 3). Comparison of these growth rate estimates with the population growth rate calculated from annual abundances during the study period revealed that the larger matrix based on statistical modeling more accurately predicted the observed trends in all but Reservoir Creek population, for which both structures produced identical estimates (Figure 3). However, both model structures performed poorly and overestimated growth rate particularly in Sheep Corral Gulch population (Figure 3). In addition to higher accuracy, the larger matrix tended to be more precise in two of four populations (Sheep Corral Gulch, Haynes Creek), resulting in narrower confidence intervals for stochastic population growth rate (Figure 3).

When matched to equivalent life stages, estimates of observed stochastic stage distributions were qualitatively identical between the two matrix structures in all populations, although they often differed significantly nearly for all life stages (Figure 4).

The proportion of realized variation in population growth rate that was due to the variability of vital rates over time was generally unaffected by matrix structure in the four study populations (Figure 5a). The estimate of realized variation in population growth rate that was due to the variability of population stage structure was clearly sensitive to matrix structure in two out of four populations (Sheep Corral Gulch, McDevitt Creek), with the larger matrix resulting in a stronger correlation between observed growth rate and the variability of stage structure than the smaller matrix (Figure 5b).

4 | DISCUSSION

The ability of structured demographic models to accurately predict population dynamics has been debated (e.g., Beissinger & Westphal, 1998; Ellner, Fieberg, Ludwig, & Wilcox, 2002), with previous studies primarily focusing on issues related to data quality, the length of the prediction interval and density dependence (e.g., Beissinger & Westphal, 1998; Crone et al., 2013; Doak, Gross, & Morris, 2005; Gross, 2002; Münzbergová & Ehrlén, 2005; Rueda-Cediel, Anderson, Regan, & Regan, 2018). However, model structure itself has received less attention despite the fact that structured models (matrix

models in particular) are usually constructed based on expert opinion with limited objective guidelines for choosing categories. In the present study, we assessed the consequences of two published matrix structures (the 4×4 matrix based on expert opinion and the 10×10 based on statistical modeling) for estimates of vital rates and predictions of stochastic population dynamics of the long-lived herb, *A. scaphoides*. In contrast to our prediction, matrix structure had a negligible effect on the accuracy or precision of binary vital rates (estimated using GLMMs) for the study species suggesting that the larger sample size per stage category (and reduced sampling error) in the 4×4 matrix did not improve the estimates of vital rate. This finding may be due to increased heterogeneity among individual plants within each category in the smaller matrix (i.e., larger distribution error), which leveled off the positive effect of decreased sampling error on vital rates. These two types of error are usually adversely affected by matrix dimension; distribution error tends to increase with increasing matrix dimension, while sampling error tends to decrease (Vandermeer, 1978).

4.1 | Model structure can affect predictions of stochastic population dynamics

Our findings suggest that the statistical comparison of all vital rates simultaneously between alternative matrix structures is not necessarily informative about population-level consequences; the lack of statistically significant differences in the accuracy and precision of vital rates between matrix structures still resulted in different estimates of stochastic population growth rates for *A. scaphoides*. The larger 10×10 matrix based on statistical modeling produced lower estimates of stochastic population growth rates for three out of four populations of *A. scaphoides* than the smaller 4×4 matrix based on expert opinion. This result somewhat contrasts with previous studies that have found stochastic population growth rate to be insensitive to matrix dimension (Picard & Liang, 2014; Tenhumberg et al., 2009). However, our result is in line with findings for perennial plants (Ramula et al., 2009; Ramula & Lehtilä, 2005; Rojas-Sandoval & Meléndez-Ackerman, 2013), which have reported growth rates to decrease with increasing matrix dimension, with larger matrices being often more accurate and precise. In the present study, the larger matrix more accurately predicted observed trends in population abundances in three out of four populations and produced also more precise estimates in two of them. The higher model accuracy and precision are probably due to the larger matrix describing the life-cycle of the study species in more detail by distinguishing new recruits from older vegetative plants, while these life stages are pooled in the smaller matrix (Figure 1). Such pooling can result in increased heterogeneity within stage categories (Vandermeer, 1978), which overestimates the survival and growth of these new recruits. A visual assessment of different vital rates reveals that the smaller matrix indeed produced a considerably higher estimate for the transitions from small and large vegetative plants to large vegetative plants (pL_S, pL_L) than the larger matrix in all four study populations (Figure 2), which might have had an additive effect on population dynamics, leading to the differences in stochastic population growth rates. Moreover, for the smaller matrix, parameter uncertainty included in the stochastic simulations resulted in overestimates of many vital rates compared to their average values estimated across years (Figure S1 in Supporting Information; results shown for the 4×4 matrix only).

The consequences of biased estimates of vital rates for stochastic population dynamics partially depend on the sensitivity of population growth rate to given vital rates. The low precision of a vital rate with high sensitivity to relative perturbations usually has the most dramatic impact on population estimates (Gross, 2002). For example, population dynamics of declining populations of long-lived perennial herbs, such as those of *A. scaphoides*, tend to be more sensitive to proportional changes in survival than those in growth and fecundity (de Kroon, van Groenendael, & Ehrlén, 2000; Oostermeijer, Brugman, de Boer, & den Nijs, 1996). It should be noted though that both matrix structures failed to predict stochastic population growth rate in one of four study populations and produced over-optimistic estimates of population viability compared to observed growth rates estimated from population abundances. Such a mismatch between the observed and predicted population growth rates might be due to ignoring temporal autocorrelation in vital rates (i.e., the environment was assumed to vary randomly over time). Since *A. scaphoides* tends to reproduce in alternate years (Crone, 2013; Crone & Lesica, 2004; Lesica, 1995), some vital rates might exhibit a negative temporal autocorrelation. Although negative temporal autocorrelation usually alleviates the effect of environmental variation on population dynamics (Lande, Engen, & Saether, 2003, p. 34), the opposite has been reported for rare perennial plants, in which it reduces population growth rate (Buckley et al., 2010).

In addition to population growth rate, matrix structure may influence other population parameters. For example, Tenhumberg et al. (2009) observed that the magnitude of transient dynamics increased with increasing matrix dimension in pea aphids, and Stott, Franco, Carslake, Townley, and Hodgson (2010) found the same pattern in plants. Moreover, in their synthesis across different plant species, McDonald et al. (2016) detected that the proportion of realized variation in growth rate due to the variability of vital rates over time was negatively associated with matrix dimension, whereas the proportion of realized variation due to the

variability of stage structure was positively associated with matrix dimension. Overall, these previous findings suggest that the dependence between the estimates of realized variation in growth rate and matrix size might be a methodological artifact. However, our study based on the two matrix structures for the same plant species did not reveal such clear relationships between the two components of realized variation of population growth rate and matrix dimension. We detected that the variability of population stage structure increased with increasing matrix dimension in only two out of four populations indicating greater importance of transient dynamics. Nevertheless, we acknowledge the fact that our results are based on two matrix structures (that also have different dimensions) for a single long-lived perennial herb, and therefore, more studies on different species with multiple matrix dimensions are required to assess methodological artifacts (if any) in population estimates due to model structure.

4.2 | Recommendations for choosing model structure

A state variable that correlates with vital rates is a key for structured population models; usually age or size for animals and size or stage for plants (Caswell, 2001; Merow et al., 2014; Morris & Doak, 2002). Previous studies can be used to inform about a potential state variable before data collection. While the model structure is greatly determined by the biology of a given species as well as study aims, our results indicate that statistical modeling can be helpful for choosing between alternative model structures. Similar to previous studies, we recommend considering multiple, biologically meaningful model structures (Beissinger & Westphal, 1998; Morris & Doak, 2002, p. 453) and testing their underlying assumptions statistically. In other words, statistics are used to explore the variability of vital rates between adjacent or alternative categories before deciding the model structure. Statistically significant differences in vital rates between adjacent categories in a structured population model clearly justify separate categories (Gremer et al., 2012; Jäkäläniemi et al., 2011), while in the opposite situation pooling might be possible, given that the structure still reflects the biology of the species. For example, Gremer et al. (2012) used GLMMs to determine the number of dormant stages for the matrix model of *A. scaphoides* by assessing whether demographic state before prolonged dormancy affected the fate of dormant plants in the following year and necessitated more than a single dormant stage. Similarly, categories for newly recruited plants were defined by comparing their vital rates to those of older plants (Gremer et al., 2012). Although our example in the present study comes from plant matrix models, the same principles apply to more recently developed integral projection models (IPMs, Easterling, Ellner, & Dixon, 2000), which have become increasingly popular in plant and animal studies (e.g., Coulson, Tuljapurkar, & Childs, 2010; Griffith, 2017; Merow et al., 2014; Ramula et al., 2009; Williams & Crone, 2006). These models may contain a combination of one or several continuous (e.g., size, biomass) and discrete variables (e.g., seed bank) that are used to describe individuals' state, resulting in a large matrix after discretization that preserves the continuous states (reviewed in Merow et al., 2014). As an example, one may need to decide whether to include one or multiple discrete categories in an IPM for the youngest life stages (Merow et al., 2014). For IPMs that are based on continuous state variables only, model structure is not an issue, and such models thus avoid potential problems related to model building. Unfortunately, continuous size data were not recorded in this long-term study, which was originally designed and initiated in 1986, long before IPMs were an option, so we cannot compare IPMs to the matrix modeling approaches used in this study for *A. scaphoides*. Regardless, matrix models and IPMs are becoming a more popularized and accessible tool for understanding the life history and informing management of populations. Therefore, we urgently need more studies evaluating the consequences of matrix construction as well as providing good general guidelines to avoid incorrect conclusions about population dynamics.

Although matrix dimension per se was not our primary interest, the present study provides some insights into comparative demographic studies. Namely, our findings add to the growing evidence of the importance of considering matrix dimension in increasing the accuracy of model outputs in comparative studies (e.g., Gamelon et al., 2014; McDonald et al., 2016; Stott et al., 2011). This improved accuracy can be achieved by including matrix dimension as a covariate in analyses that are based on matrix models from a large number of species (McDonald et al., 2016; Stott et al., 2011) or by using different matrix collapsing or standardization techniques (Gamelon et al., 2014; Salguero-Gómez & Plotkin, 2010).

In summary, the present study indicates that while matrix structure may not matter for estimates of some population parameters (e.g., the accuracy and precision of vital rates and stochastic stable stage distribution), it may affect estimates of stochastic population growth rate. In such cases, statistical modeling to choose model structure might predict population trends more accurately than a model constructed based on expert opinion. Overall, a modeling approach provides a more objective way for designing matrix population models than expert opinion and can be preferable particularly when the biology of the study species is poorly known.

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CONFLICT OF INTEREST

We declare that we have no conflict of interest.

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SUPPORTING INFORMATION

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