Causes and consequences of variation in plant population growth rate: a synthesis of matrix population models in a phylogenetic context

Abstract
Explaining variation in population growth rates is fundamental to predicting population dynamics and population responses to environmental change. In this study, we used matrix population models, which link birth, growth and survival to population growth rate, to examine how and why population growth rates vary within and among 50 terrestrial plant species. Population growth rates were more similar within species than among species; with phylogeny having a minimal influence on among-species variation. Most population growth rates decreased over the observation period and were negatively autocorrelated between years; that is, higher than average population growth rates tended to be followed by lower than average population growth rates. Population growth rates varied more through time than space; this temporal variation was due mostly to variation in post-seedling survival and for a subset of species was partly explained by response to environmental factors, such as fire and herbivory. Stochastic population growth rates departed from mean matrix population growth rate for temporally autocorrelated environments. Our findings indicate that demographic data and models of closely related plant species cannot necessarily be used to make recommendations for conservation or control, and that post-seedling survival and the sequence of environmental conditions are critical for determining plant population growth rate.

Keywords
Comparative analysis, demography, fire, herbivory, matrix population models, MCMCglmm, population dynamics, population growth rate, spatial and temporal variation, temporal autocorrelation.

INTRODUCTION
In nearly all natural systems, environmental conditions fluctuate over time. This environmental variation influences population growth rates and consequently species abundance and distribution. Environmental variation is typically thought to elevate extinction risk. However, in perennial plants with high adult survivorship, environmental variation...
that leads to rare episodes of high recruitment may promote persistence (Higgins et al. 2000). Understanding how population growth rate varies in space and time in natural plant populations, and identifying the sources of that variation is fundamental to predicting species responses to environmental change (e.g. climate change) and other environmental factors (Gotelli & Ellison 2006; Morris et al. 2008; Dahlgren & Ehrén 2009; Dalgleish et al. 2010).

Variation in population growth rates is due to differences in underlying vital rates, such as birth, growth, reproduction and death. Vital rates are in turn influenced by multiple environmental factors (e.g. fire, herbivores, weather) and their contributions to population dynamics depend on the life history of the focal species (Silvertown et al. 1993, 1996; de Kroon et al. 2000; Ramula et al. 2008a). Population dynamics may vary substantially among populations and years within the same plant species (e.g. Pascarella & Horvitz 1998; Warton & Wardle 2003; Jongejans & de Kroon 2005) and this variation may be related to changes in population density. In general, we would expect average population growth rates to be stable but patterns of variation in population growth rates to differ among species. Variation in population growth rates is likely to depend on species life-form and lifespan (García et al. 2008; Dalgleish et al. 2010), with herbs and grasses more likely to exhibit variable population growth rates than trees and shrubs. If similar environmental factors cause both spatial and temporal variation, then understanding spatial variation in population dynamics might allow understanding of temporal variation, informing also under what circumstances (if any) spatial dynamics might be substitutable for temporal dynamics.

In randomly fluctuating environments, vital rates are expected to vary from year to year in an unpredictable way. However, in many natural environments fluctuations occur non-randomly over a longer period of time causing significant temporal autocorrelation. For example, succession results in a sequence of environmental conditions and positive temporal autocorrelation in vital rates (e.g. Pascarella & Horvitz 1998). Temporal autocorrelation can also be negative such that a good year is followed by a bad year, for instance, because of synchronized flowering and associated costs of reproduction (Crone et al. 2009). Due to the rarity of long-term demographic studies for plants (Menges 2000), temporal autocorrelation is rarely included in predictions of population performance (but see Pascarella & Horvitz 1998; Quintana-Ascencio et al. 2003; Menges et al. 2006), although in some cases, it has been shown to have a large effect on predicted population dynamics (Pike et al. 2004; Tuljapurkar & Haridas 2006).

Vital rates are most commonly linked to population growth rate using matrix population models that describe individuals classified by age, size or life-stage moving through the life-cycle (Caswell 2001). Due to similar construction and standard parameter estimation, matrix population models have been widely used to quantify population dynamics across plant species with different life-histories, including rare and invasive species (e.g. Silvertown et al. 1993, 1996; Ramula et al. 2008a; Burns et al. 2010). A large and growing number of techniques exist for incorporating variation in vital rates into population growth rate estimates (Tuljapurkar 1990; Fieberg & Ellner 2001; Kaye & Pyke 2003; Tuljapurkar et al. 2003; Doak et al. 2005b; Dahlgren & Ehrén 2009). However, fewer studies have to date examined the sources of variation and the importance of realized levels of vital rate variation for population growth rates of natural populations.

Closely related species often show more similarity in their traits or geographic distributions than less related species (e.g. Darwin 1859; Garland et al. 1993; Freckleton et al. 2002; Blomberg et al. 2003; Cadotte et al. 2009; Diez et al. 2009), and may therefore be expected to have more similar population dynamics than non-related species, making phylogeny a potential predictor of patterns of variation in vital rates and population growth rates. It is possible to predict patterns of variation in population growth rate based on species relatedness, phylogeny might be a useful tool for identifying species that are likely to become endangered or invasive, and for designing management when detailed demographic information is not available. However, most studies examining variation in plant population growth rate have focused on a single or a few species and we do not know enough about variation above the species level to be able to say whether phylogeny is an important predictor of population dynamics.

We constructed a database of demographic models with both spatial and temporal replication from 50 species of terrestrial plants and a corresponding phylogeny to examine how potential sources of variation (e.g. vital rates, phylogeny, life-form, rare or common distribution, environmental factors) influence population growth rates. We asked the following specific questions: (i) How do plant population growth rates vary within species and among species, and how does phylogeny contribute to that variation? (ii) What are the sources of variation in population growth rates? We examine how temporal variation in vital rates (survival, growth, fecundity) contributes to population growth rate, and how rare or common distribution, population density and environmental factors (fire, herbivory) are related to variation in population growth rate. (iii) What is the importance of realized temporal variation in population growth rates to predicted population dynamics? We compare deterministic and stochastic population growth rates and examine the role of temporal autocorrelation. If realized temporal variation in population growth rates is unimportant, we would expect...
average deterministic growth rate to be similar to stochastic population growth rate.

We found that populations within a species are more similar to each other than populations among species, with a minimal influence of phylogeny above the species level. Our findings indicate that the population growth rate of any particular species cannot be substituted for that of a closely related species to predict population dynamics. Most plant populations studied had a decreasing trend in population growth rates over the observation period and population growth rates between years were negatively autocorrelated. Population growth rates varied more through time than space regardless of life-form. Temporal variation in a subset of species for which we had environmental data was partly explained by time-since-fire and herbivory. Deterministic and stochastic population growth rates were highly correlated for randomly fluctuating environments but differed for temporally autocorrelated environments, particularly for rare species with strong positive or negative autocorrelations. Our results raise new questions about the causes and consequences of temporal variation in vital rates, and suggest that simple population models with uncorrelated environmental variation may not adequately capture stochastic population dynamics for strongly autocorrelated environments.

### METHODS

We first summarize our database on matrix population models and variables calculated to analyse population dynamics. We then describe statistical analyses used to answer the three main questions addressed above.

### Database

The database, obtained from the literature and some unpublished material from the authors and their collaborators, contains matrix population models for 50 perennial plant species in which multiple populations (≥ 2) and multiple matrices per population (≥ 2) were available. A total of 708 matrices for 38 herbaceous species (herbs and grasses) and 120 matrices for 12 other species (trees, shrubs and succulents) was assembled. This database is unique as it includes both spatial and temporal population dynamics for each species, allowing a detailed comparison within and among species. Different subsets of the data were used for analyses depending on which data were available (detailed under specific analyses outlined below). Species were categorized as common (including three invasive species) or rare, or as common, restricted range rare and wide range rare (i.e. locally rare but regionally widespread), depending on the analysis. Species were classified based on the author’s description. Matrix dimension was recorded at the species level as a factor with three levels, small (≤ 4 matrix dimensions), medium (≤ 7) and large (≥ 7); category boundaries were chosen to ensure adequate replication within each category. Treating matrix dimension as a categorical variable enabled simpler interpretation of interactions than treating it as a continuous variable with polynomial terms. Species were also classified as clonal or not and having a seedbank or not. Spatial locations of populations were sourced from the literature where available and through personal communications with the authors.

### Calculation of variables

Population matrices were analysed using standard methods (Cochran & Ellner 1992; Caswell 2001), implemented within a custom built MATLAB program 7.1 (The MathWorks, Inc., Natick, MA, USA). In cases where the original papers incorporated a seedbank incorrectly leading to a spurious one-year delay in the life-cycle (Silvertown et al. 1993: p. 467; Caswell 2001: p. 61), the matrix was corrected before analysis was carried out. In a few species, some matrices were reducible (Caswell 2001) because a matrix element involving growth from one of the smallest stages was zero. In these cases, we added a small value (10⁻²⁰) to the matrix (Ehrln & Lehtilä 2002).

### Variation and sources of variation in population growth rates

For analyses of variation in population growth rates within and among species, we used a subset of data for each species in which the same consecutive years were surveyed for every population (i.e. if some populations were studied longer than others for a species, only a subset of the data were used; this reduced our data set to 49 species, 197 populations, totalling 736 matrices; Table S1). This avoids confounding spatial and temporal variation, gives a clearer comparison of whether spatial or temporal variation in population growth rates is greater and allows straightforward interpretation of temporal autocorrelation. We calculated the long-term deterministic population growth rate \( \log \hat{\lambda}_{\text{det}} \) for each matrix according to Caswell (2001, p. 108) and estimated standard deviation of population growth rates across years for each population \( \sigma \log \hat{\lambda}_{\text{det}} \). Based on all annual matrices from each population, we calculated standard deviation for five demographic rates (hereafter denoted vital rates) across years: post-seedling survival, growth to stages with a greater reproductive value conditional on survival, retrogression to stages with a lower reproductive value conditional on survival, the number of seeds entering the seedbank and the number of seedlings produced. Post-seedling survival was estimated as the weighted mean of the survival of individuals not included in the seed bank or the first non-seed stage (often...
Importance of temporal variation in plant population growth rates

The full 50 species dataset and all available populations with multiple years were used. For each population of each species, we constructed a mean matrix by averaging multiple annual matrices and calculated deterministic population growth rate (log \( \lambda_{\text{mean}} \)). This estimate is based on average vital rates over time and can sometimes be used to describe average population performance (Doak et al. 2005a). However, mean matrix population growth rate often differs from the long-term stochastic population growth rate (Tuljapurkar et al. 2003; Boyce et al. 2006), and differences between these two rates can be regarded as a measure of the influence of temporal variation in vital rates on population growth rates.

To examine the importance of temporal variation in plant population growth rates to predicted population dynamics, we compared log \( \lambda_{\text{mean}} \) to stochastic population growth rates calculated for randomly fluctuating environments. We calculated stochastic population growth rates for each population using a simulation which started from the stable stage distribution derived from the mean matrix with 1000 individuals. All simulations were based on a matrix selection method which is suitable for a small number of matrices (Ramula & Lehtilä 2005). In these simulations, each matrix had an equal probability of being selected at each time step and population dynamics were predicted for 500 years with 10 000 iterations per year. Stochastic population growth rate (\( \lambda_s \)) was calculated as log[\( (N_t/N_0)^{1/T} \)], where \( N \) is population size at time \( t \) (Caswell 2001). In addition to the simulations, we used Tuljapurkar’s analytical approximation for uncorrelated environments (Caswell 2001; eq. 14.72), which estimates the stochastic population growth rate (\( \lambda_{\text{stoch}} \)) from observed matrices and covariances among matrix entries. This method provides an alternative to simulations but may not describe population dynamics accurately if there is a lot of variation in vital rates over time (Morris & Doak 2002).

Both the simulation and Tuljapurkar’s method ignore temporal autocorrelation, assuming uncorrelated population growth rates over time. To estimate population growth rates for temporally autocorrelated environments, we used matrices from each population in the same sequence they were observed in the field and calculated population growth rate (\( \lambda_{\text{seq}} \)) by taking the \( n \)-th root of the greatest positive eigenvalue of the matrix product \([A_nA_{n-1}...A_1]\) where \( A \) denotes annual matrices over time and \( n \) the total number of matrices per population. Throughout the paper, we use log-transformed mean matrix growth rates to enable comparisons between them and stochastic population growth rates, with population growth rates \( < 0 \) denoting decreasing populations and population growth rates \( > 0 \) denoting increasing populations.

Analyses

Variation in population growth rates within species and among species

To examine the effect of phylogeny on variation in population growth rates, we generated a phylogeny using the seed plant phylogeny available via phylomatic (reference tree #R20050610), which references the angiosperm phylogeny website, the most recent, and constantly updated, summary of the angiosperm phylogeny available (phylomatic version 2; Webb C.O. 2005; Webb et al. 2008; Stevens 2009). This topology was then assigned branch lengths based on fossil calibration following Wikström et al. (2001) using the bladj command in phylcom (version 4.0.1b), which approximates branch lengths in millions of years (Webb et al. 2008; see Fig. S1).

As we had multiple levels of random effects: species within a phylogeny, populations within species and years
within populations, we used the R library MCMCglmm v.1.10 to test for effects of phylogeny. MCMCglmm is a Markov chain Monte Carlo sampler for multivariate generalized linear mixed models with special emphasis on correlated random effects arising from pedigrees and phylogenies (Hadfield & Nakagawa 2010). MCMCglmm enables the inclusion of a phylogeny, equivalent to a pedigree in quantitative genetics studies, as a variance/co-variance matrix in a generalized linear modelling Bayesian framework. The MCMCglmm model also enables random effects to be fit at the species and below species levels. We fit species and populations nested within species as random effects for models of deterministic population growth rate (log $\lambda_{\text{det}}$), and a random effect of species for models of standard deviation of population growth rate ($\sigma_{\log \lambda_{\text{det}}}$) and comparisons of mean matrix and stochastic population growth rate. We used weak proper priors on the grouping variables (variance $\nu > 0$, degree of belief $n = 1$) and assessed an arbitrary range of different values for the prior variances ($0.001 - 1$). We also assessed the effect of prior selection on datasets where the response variable was randomized. The adequacy of models with and without phylogeny was assessed by comparing the Deviance Information Criterion (DIC) of the two models (Spiegelhalter et al. 2002).

The phylogenetic effects have expected (co)variances proportional to the phylogenetic covariance matrix constructed from the phylogenetic tree (Fig. S1) for the MCMCglmm models (Hadfield & Nakagawa 2010). The within group errors were assumed to be independent and identically normally distributed (IID), with mean 0 and variance $\sigma^2$, except where a within group correlation structure was explicitly applied. The random effects were also assumed to be IID for different groups, with mean 0 and covariance matrix $\Psi$. IID assumptions for residuals and random effects were assessed using plots of the within group errors and random effects (Pinheiro & Bates 2000: p. 174–196). Chains mixed well with little autocorrelation, indicating good convergence.

We examined the effect of phylogeny on population growth rate (log $\lambda_{\text{det}}$) using a model which included all predictors (see Table 1) as well as a simpler version of the model which only retained significant terms from the non-phylogenetic models (see below). Autocorrelation of errors to account for autocorrelation between time periods within a population could not be fitted in the MCMCglmm models for testing phylogeny and was therefore omitted. Similarly, we examined the effect of phylogeny on standard deviation of population growth rate ($\sigma_{\log \lambda_{\text{det}}}$) and stochastic population growth rate ($\hat{\lambda}_s$, $\hat{\lambda}_{\text{Fudi},s}$, $\lambda_{\text{seq}}$) using a model which included several predictors and variance at the species level (see Tables 2 and 3 for predictors fitted).

**Table 1** Predictor variables and their significance in non-phylogenetic models for deterministic population growth rate, log $\lambda_{\text{det}}$. Variables retained in the simplest adequate model are in bold. Fixed effects were assessed using likelihood ratio tests and maximum likelihood estimates. Random effects were assessed using likelihood ratio tests and restricted maximum likelihood estimates. The random effect of species was not tested as populations were nested within species and were retained in the model. Data were from 49 species.

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>LR test$_{d.f.}$, $P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>LR$_1$ = 10.7, &lt; 0.005</td>
</tr>
<tr>
<td>Matrix dimension (small, medium, large)</td>
<td>LR$_2$ = 0.4, &lt; 0.85</td>
</tr>
<tr>
<td>Life-form (herb, other)</td>
<td>LR$_1$ = 0.7, &lt; 0.5</td>
</tr>
<tr>
<td>Clonality (binary)</td>
<td>LR$_1$ = 0.1, &lt; 0.96</td>
</tr>
<tr>
<td>Seedbank (binary)</td>
<td>LR$_1$ = 1.5, &lt; 0.3</td>
</tr>
<tr>
<td>Distribution (common, rare restricted, rare widespread)</td>
<td>LR$_2$ = 0.1, &lt; 0.95</td>
</tr>
<tr>
<td>Year : life-form</td>
<td>LR$_1$ = 2.1, &lt; 0.2</td>
</tr>
<tr>
<td>Year : clonality</td>
<td>LR$_1$ = 3.2, &lt; 0.3</td>
</tr>
<tr>
<td>Year : seedbank</td>
<td>LR$_1$ = 2.5, &lt; 0.2</td>
</tr>
<tr>
<td>Year : distribution</td>
<td>LR$_2$ = 2.6, &lt; 0.3</td>
</tr>
<tr>
<td>$\sigma^2_{\text{species}}$ (intercept)</td>
<td>Not tested</td>
</tr>
<tr>
<td>$\sigma^2_{\text{population}}$ (intercept)</td>
<td>LR$_2$ = 39.5, &lt; 0.0001</td>
</tr>
<tr>
<td>$\sigma^2_{\text{population}}$ (slope of year)</td>
<td>LR$_2$ = 11.4, &lt; 0.004</td>
</tr>
<tr>
<td>Autocorrelation of residuals (AR1)</td>
<td>LR$_1$ = 20.7, &lt; 0.0001</td>
</tr>
</tbody>
</table>

**Sources of variation in population growth rates**

As the inclusion of phylogeny was not supported for models of population growth rate (log $\lambda_{\text{det}}$) (see Results and Table S2), we used models without phylogeny to test hypotheses about the structure and partitioning of variation between spatial and temporal components for log $\lambda_{\text{det}}$. Simple variance components analysis of log $\lambda_{\text{det}}$ was used initially to assess the effects of population level vs. year level random effects (nested within species) to determine the relative contributions of spatial vs. temporal effects. Population and year effects could not be included in the same model due to the lack of replicates at the within population, within year level. As population level variation may partly depend on spatial distances among the study populations with populations closer together exhibiting more similar dynamics, we also fitted models only including species with populations at least 1 km apart (24 species) to explore the effect of spatial distances among the populations on variation in population growth rates (i.e. whether the results differ from those when all populations are included).

To better model temporal effects on population growth rate, we constructed a general linear mixed effects model which included a fixed effects structure, a random effects structure and autocorrelation between errors for sequences of years within a population. For all of the following non-phylogenetic linear mixed effects models, random
Table 2 Predictor variables and their significance in non-phylogenetic models for standard deviation of population growth rate, $\sigma_{\text{log } \lambda_{\text{mean}}}$: Variables retained in the simplest adequate model are in bold. Fixed effects were assessed using likelihood ratio tests and maximum likelihood estimates. Random effects were assessed using likelihood ratio ratio tests and restricted maximum likelihood estimates. The random effect of species was not tested as populations were nested within species and were retained in the model. There were missing data for Campanula americana, Alnus incana and Astragalus alpestrinus, models were therefore run including 47 species. Note that simplified models including $\log \sigma_{\text{growth}}$ instead of $\log \sigma_{\text{survival}}$ were structurally identical; however, models with $\log \sigma_{\text{survival}}$ were strongly preferred to models with $\log \sigma_{\text{growth}}$ ($\Delta$AIC > 10).

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>LR test</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda_{\text{mean}}$</td>
<td>$LR_1 = 10.1, &lt; 0.002$</td>
<td></td>
</tr>
<tr>
<td>Matrix dimension (small, medium, large)</td>
<td>$LR_1 = 4.3, &lt; 0.2$</td>
<td></td>
</tr>
<tr>
<td>Distribution (common, rare restricted, rare widespread)</td>
<td>$LR_1 = 0.01, &lt; 0.95$</td>
<td></td>
</tr>
<tr>
<td>No. matrices per population</td>
<td>$LR_1 = 6.0, &lt; 0.015$</td>
<td></td>
</tr>
<tr>
<td>Life-form (herb, other)</td>
<td>$LR_1 = 0.2, &lt; 0.7$</td>
<td></td>
</tr>
<tr>
<td>Seedbank (binary)</td>
<td>$LR_1 = 0.8, &lt; 0.4$</td>
<td></td>
</tr>
<tr>
<td>$\log \sigma_{\text{survival}}$</td>
<td>$LR_1 = 28.0, &lt; 0.0001$</td>
<td></td>
</tr>
<tr>
<td>CV fecundity</td>
<td>$LR_1 = 1.7, &lt; 0.2$</td>
<td></td>
</tr>
<tr>
<td>$\sigma^2_{\text{species}}$ (intercept)</td>
<td>Not tested</td>
<td></td>
</tr>
<tr>
<td>$\sigma^2_{\text{population}}$ (intercept)</td>
<td>Not tested</td>
<td></td>
</tr>
<tr>
<td>$\sigma^2_{\text{population}}$ (slope of $\log \sigma_{\text{survival}}$)</td>
<td>$LR_2 = 13.6, &lt; 0.0015$</td>
<td></td>
</tr>
</tbody>
</table>

Table 3 Non-phylogenetic models for three measures of stochastic population growth rate ($\lambda_n$, $\hat{\lambda}_{\text{Tulja}}$ and $\lambda_{\text{seq}}$) for 50 species. Variables retained in the simplest adequate model are in bold. Fixed effects were assessed using likelihood ratio tests and maximum likelihood estimates. Random effects were assessed using likelihood ratio tests and restricted maximum likelihood estimates. Some explanatory variables were not tested because of significant interactions.

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>$\lambda_n$</th>
<th>$\hat{\lambda}_{\text{Tulja}}$</th>
<th>$\lambda_{\text{seq}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\log \lambda_{\text{mean}}$</td>
<td>Not tested</td>
<td>$LR_2 = 8.2, P &lt; 0.002$</td>
<td>$LR_1 = 111.2, P &lt; 0.001$</td>
</tr>
<tr>
<td>Matrix dimension (small, medium, large)</td>
<td>$LR_1 = 1.35, P &lt; 0.3$</td>
<td>$LR_2 = 6.3, P &lt; 0.05$</td>
<td>$LR_2 = 6.4, P &lt; 0.05$</td>
</tr>
<tr>
<td>No. years per population</td>
<td>$LR_1 = 0.26, P &lt; 0.7$</td>
<td>$LR_2 = 0.26, P &lt; 0.7$</td>
<td>$LR_1 = 0.3, P &lt; 0.6$</td>
</tr>
<tr>
<td>Life-form (herb, other)</td>
<td>$LR_1 &lt; 0.0001, P &lt; 1$</td>
<td>$LR_1 = 0.07, P &lt; 0.8$</td>
<td>$LR_1 = 3.4, P &lt; 0.07$</td>
</tr>
<tr>
<td>Seedbank (binary)</td>
<td>Not tested</td>
<td>$LR_2 = 8.2, P &lt; 0.005$</td>
<td>Not tested</td>
</tr>
<tr>
<td>Distribution (common, rare)</td>
<td>Not tested</td>
<td>$LR_1 = 1.3, P &lt; 0.3$</td>
<td>$LR_1 = 1.7, P &lt; 0.2$</td>
</tr>
<tr>
<td>$\log \lambda_{\text{mean}}$ : no. years per pop</td>
<td>$LR_1 = 0.04, P &lt; 0.85$</td>
<td>$LR_2 = 4.0, P &lt; 0.2$</td>
<td>$LR_2 = 0.08, P &lt; 0.96$</td>
</tr>
<tr>
<td>$\log \lambda_{\text{mean}}$ : matrix dimension</td>
<td>$LR_1 = 0.75, P &lt; 0.7$</td>
<td>$LR_1 = 0.64, P &lt; 0.5$</td>
<td>$LR_1 = 0.04, P &lt; 0.9$</td>
</tr>
<tr>
<td>$\log \lambda_{\text{mean}}$ : life-form</td>
<td>$LR_1 = 0.4, P &lt; 0.6$</td>
<td>$LR_1 = 1.8, P &lt; 0.2$</td>
<td>$LR_1 = 1.3, P &lt; 0.3$</td>
</tr>
<tr>
<td>$\log \lambda_{\text{mean}}$ : seed bank</td>
<td>$LR_1 = 0.21, P &lt; 0.7$</td>
<td>$LR_1 = 2.3, P &lt; 0.2$</td>
<td>$LR_1 = 13.1, P &lt; 0.001$</td>
</tr>
<tr>
<td>$\sigma^2_{\text{species}}$ (intercept)</td>
<td>Not tested</td>
<td>$LR_2 = 5.0, P &lt; 0.003$</td>
<td>Not tested</td>
</tr>
<tr>
<td>$\sigma^2_{\text{species}}$ (slope of $\log \lambda_{\text{mean}}$)</td>
<td>$LR_2 = 20.7, P &lt; 0.001$</td>
<td>$LR_2 = 33.8, P &lt; 0.001$</td>
<td>$LR_2 = 56.7, P &lt; 0.001$</td>
</tr>
</tbody>
</table>
on population growth rate across species. We also tested for autocorrelation between years. As time-since-fire and year were confounded, we did not include year in the fire model. For the herbivory model, we included year as a fixed effect and variance about the slope of year as a random effect to account for possible temporal trends. We note that all three species with data available for fire were from the same geographic region (Central Florida, USA). We examined the effect of habitat on log $\lambda_{\text{det}}$. Habitat data were available for 483 matrices and two categories of habitat had sufficient species level replicates, grassland (15 species, 53 populations) and forest (18 species, 86 populations). Finally, we tested whether density affected log $\lambda_{\text{det}}$ for a subset of 207 matrices (21 species, 58 populations). We constructed models including density, year and random effects of species and population (with variance about the intercept and slope of density at the population level to account for context specific effects of density) with autocorrelation of errors (AR1) for sequences of years within populations.

For analyses of standard deviation in population growth rate, $\sigma_{\log \lambda_{\text{det}}}$ we used the same predictors as for analyses of log $\lambda_{\text{det}}$ (see Table 2 for predictors). In addition, we examined the contributions of temporal variation in vital rates (standard deviation of survival and growth and CV of fecundity) in a subset of species ($n = 47$) for which these data were available. Plots and initial modelling indicated that variation in survival and growth (log $\sigma_{\text{survival}}$ and log $\sigma_{\text{growth}}$) were co-linear, therefore the sources of variation in population growth rates was analysed using a model which included the predictors in Table 1 and either log $\sigma_{\text{survival}}$ or log $\sigma_{\text{growth}}$, the better predictor was assessed using AIC. The random effects structure included variance about the intercept and about the slope of log $\sigma_{\text{survival}}$ or log $\sigma_{\text{growth}}$ at the species level. As phylogeny was not important, we used linear mixed effects models (nlme library in R).

**Importance of temporal variation in population growth rates**

To examine the importance of realized temporal variation in plant population growth rate for randomly fluctuating environments, we compared mean matrix population growth rate (log $\lambda_{\text{mean}}$) to stochastic population growth rates ($\lambda_{\text{seq}}$ and $\lambda_{\text{Fujita}}$), and further examined the role of temporal autocorrelation in plant population dynamics by comparing mean matrix population growth rate to $\lambda_{\text{seq}}$. As the inclusion of phylogeny was not supported in any of the models (see Results), we used linear mixed effects models (lme4 library in R to ensure model convergence) with variance about the intercept and the slope of mean matrix population growth rate (log $\lambda_{\text{mean}}$) with species as a random effect to estimate model parameters (Table 3).

To determine whether the magnitude of the temporal autocorrelation explained differences between stochastic population growth rates for randomly fluctuating and temporally autocorrelated environments, we constructed a model for a subset of species with at least three consecutive matrices ($n = 26$) with $\lambda_{\text{seq}}$ as a response variable and the following explanatory variables: $\lambda_{\text{seq}}$, temporal autocorrelation of annual population growth rates (as linear and quadratic effects), distribution (rare, common) and their interactions. Species was used as a random effect.

Normality and homogeneity assumptions were examined for each model visually from residual plots and were well supported. Exceptions were models of stochastic population growth rates, where the differences between mean matrix and stochastic population growth rates were mostly in one direction only, leading to asymmetric distribution of residuals. However, fitting heterogeneous variances by species distribution (common/rare) or matrix dimension was not supported by LR tests, indicating that the model assumptions about homogenous variances were not severely violated.

**RESULTS**

**Variation in population growth rates within species and among species**

The effect of phylogeny on all response variables was weak, i.e. the phylogenetic relationship between species was unrelated to deterministic population growth rate, standard deviation of population growth rate, or the relationship between mean matrix and stochastic population growth rates. In analyses of deterministic population growth rate (log $\lambda_{\text{det}}$), the non-phylogenetic model was preferred ($\Delta$DIC > 7.5 for all priors tested). The proportion of variance explained by phylogeny was very sensitive to the priors selected, ranging from < 1 to 28% for the model of log $\lambda_{\text{det}}$ and was similar to that for randomized log $\lambda_{\text{det}}$ where phylogeny should convey no information (< 1–18% Table S2). A value of 0 indicates the grouping conveys no information, up to 100% where all members of a group are identical (Gelman & Hill 2007). The proportion of variance explained by species was insensitive to prior selection (c. 14% for all priors tested). Similarly, in analyses of the standard deviation of population growth rate and stochastic population growth rates, the models without phylogeny were either identical to the models with phylogeny ($\Delta$DIC < 1) or models without phylogeny were strongly preferred ($\Delta$DIC > 6.5).

**Sources of variation in population growth rates**

Populations within a year were more similar to each other than the same population across years, although this pattern depended on spatial scale and temporal autocorrelation.
Variance components analysis of population growth rate used to determine spatial and temporal effects revealed that the population level effect when nested within species was small (missing middle grey bar in Fig. 1a), whereas when year was nested within species it explained a similar amount of variance in population growth rates as species (Fig. 1a). However, when species with populations \( \geq 1 \text{ km} \) apart were analysed, the proportion of variance explained by population increased (middle grey bar in Fig. 1b), indicating that population growth rates were more similar within a population through time, i.e. the year effect weakened and the population effect strengthened. For both cases, the inclusion of autocorrelation between years increased the explanatory power at the population level and reduced the residual variance (black bars in Fig. 1a, b).

The effect of year on population growth rate (log \( \lambda_{det} \)) was significant and negative, indicating a decreasing trend in population growth rate over time (Table 1, Fig. 2 for predicted values, Table S3 for parameter estimates). Population growth rates decreased through time at different rates for different populations (Fig. 2); variance about the slope for year within population was significant (Table 1). Despite the overall negative trend in population growth rate through time most populations remained increasing (log \( \lambda_{det} > 0 \)) throughout the study (Fig. S2). Around these average trends in population growth rates, autocorrelation of annual residuals was highly significant (Table 1) and negative (\( \rho = -0.3 \)), meaning that years with higher than average population growth rates tended to be followed by years with lower than average population growth rates and vice versa. When autocorrelation of errors within populations and population-specific temporal trends were included in the model, the proportion of variance explained at the population level increased substantially relative to the simple variance components analysis (Fig. 1a, b). Appropriate modelling of within population temporal processes was therefore important.

To explore possible mechanisms for temporal autocorrelation in annual population growth rates, we examined autocorrelations (AR1, using the acf function in R) for 133 populations with > 3 years of data from consecutive years and found that autocorrelations in survival (LR1 = 14.2, \( P < 0.0005 \)) and fecundity (LR1 = 8.56, \( P < 0.004 \)) had significant additive positive contributions to autocorrelations in population growth rate.

Examination of direct relationships between vital rates and population growth rate revealed that log(survival) contributed to population growth rate significantly when tested in a model including autocorrelation of errors and varying slopes for survival (LR1 = 68.6, \( P < 0.0001 \)); varying slopes for year could not be included due to model convergence issues. Log(growth) was significant when included in a model with autocorrelation and varying slopes for year (LR1 = 5.97, \( P < 0.02 \)). Fecundity was not significant.

Both time-since-fire and herbivory intensity explained part of the temporal variation in population growth rate. There was a significant effect of the quadratic term of time-since-fire (LR1 = 19.5, \( P < 0.0001 \)), with no significant population level variation in the slope (LR1 = 0.0003 \( P > 0.9 \)) (Fig. 3). This indicates that population growth rates can be expected to decline after fire until reaching more stable dynamics. There was also a significant negative autocorrelation between years, similar in magnitude to the autocorrelation found in the full dataset (\( \rho = -0.38 \), LR1 = 15.8, \( P < 0.0001 \)). Population growth rate declined linearly with increasing herbivory intensity (herbivory: LR1 = 9.8, \( P < 0.002 \) and year: LR1 = 6.59, \( P < 0.02 \), Fig. 4). Autocorrelation of errors (LR1 = 0.6, \( P > 0.5 \)) and population level random effects (LR1 = 0.05, \( P > 0.9 \)) were not statistically significant. Models with and without habitat were very similar (\( \Delta AIC = 0.6 \)), with little support for retaining habitat in
the model for this subset of the data. Finally, our analyses revealed no evidence for density dependence in population growth rates. The random effect of varying slopes for density at the population level was not significant (LR2 < 0.001, \( P > 0.9 \)) and a fixed effect of density and habitat were also not significant (LR1 = 0.8, \( P < 0.4 \) and LR1 = 2.6, \( P < 0.1 \), respectively).

Variation in survival and growth rather than variation in fecundity explained temporal variation in population growth rates (\( \sigma \log \lambda_{det} \)). Variation in \( \sigma \log \lambda_{det} \) increased with mean population growth rate (\( \log \lambda_{mean} \)), the number of matrices and the standard deviation of survival (\( \sigma_{\text{survival}} \)) (Fig. 5, Table 2, Table S3 for parameter estimates).

**Importance of variation in population growth rates**

Mean matrix population growth rate (\( \log \lambda_{mean} \)) was a good predictor of all measures of stochastic population growth rate (\( \lambda_s \), \( \lambda_{Tulja} \) and \( \lambda_{seq} \)) (Table 3). However, mean matrix population growth rate tended to be greater relative to \( \lambda_s \) and \( \lambda_{Tulja} \) for rare species and species with medium and small matrix dimensions (Fig. 6). Departure from a 1 : 1 relationship with mean population growth rate was most
noticeable for rare species where stochastic population growth rate was calculated taking autocorrelation into account \( \lambda_{\text{seq}} \) (Fig. 6). Mean matrix and stochastic population growth rates sometimes predicted opposite population dynamics; for 14 of 222 populations (6%) log \( \lambda \) indicated an increasing population, whereas \( \lambda_{\text{seq}} \) indicated a declining population and vice versa for four of 222 populations (2%).

The contribution of temporal autocorrelation to \( \lambda_{\text{seq}} \) was nonlinear (LR1 = 9.3, \( P < 0.01 \)) for the \( \lambda \times \) quadratic autocorrelation interaction) and depended on species distribution and the magnitude of \( \lambda \) (LR1 = 20.9, \( P < 0.0001 \) for the distribution \( \times \lambda \times \) autocorrelation interaction). Both large positive and negative autocorrelations caused departure from an expected 1 : 1 relationship between \( \lambda \) and \( \lambda_{\text{seq}} \) especially for rare species (Table S6 for parameter estimates), showing that the strength of autocorrelation is important. In our dataset, the six data-points that departed most strongly from the expected 1 : 1 relationship had large negative autocorrelations and for the five rare species \( \lambda \) was substantially higher than \( \lambda_{\text{seq}} \) (Fig. 7).

**DISCUSSION**

Plant population growth rates exhibit a signal of species

For our dataset of 50 perennial plants, we found species to be an important predictor of population dynamics with phylogeny above the species level having a little or no explanatory power. This indicates that patterns of variation in plant population growth rates are evolutionarily labile above the species level for the species sampled in this study, suggesting that we cannot predict population dynamics based on phylogenetic relatedness alone. Although our database is taxonomically sparse with few species per genus, other studies using larger databases have also reported a negligible effect of phylogeny on the evolution of plant life-histories, vital rates, and hydrological niches in plant
communities (Silvertown et al. 2006; Küster et al. 2008; Burns et al. 2010); therefore, we consider the lack of a phylogenetic signal on population dynamics found here to be biologically reasonable. We note however that a more fine scale sampling of genera (i.e. a larger number of species per genus) could still reveal a phylogenetic signal on patterns of variation in population growth rates.

Although several studies have shown that phylogenetic relatedness or taxonomic groupings can be useful for predicting rarity or invasiveness (Pyšek 1998; Daehler 1998; Daehler et al. 2004; Pheloung et al. 1999; Purvis et al. 2000; Schwartz & Simberloff 2001; Diez et al. 2009; but see Lambdon 2008), our results indicate that this does not likely result from phylogenetic constraints on demography. Our results suggest that demographic data of closely related species may provide little information on demography for the management of rare or invasive species.

**Plant population growth rates decline through time**

We found a negative temporal trend in population growth rates for most of the populations. This trend held regardless

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**Figure 5** Temporal variation in population growth rate is partly explained by (a) standard deviation of survival ($\log \sigma_{\text{survival}}$), (b) the number of matrices per population and (c) mean matrix population growth rate ($\log \lambda_{\text{mean}}$). Points are observed data from populations within 47 species.

**Figure 6** Relationships between mean matrix population growth rates ($\log \lambda_{\text{mean}}$) and stochastic population growth rates ($\lambda_{\text{seq}}$, $\lambda_{\text{Tulija}}$, and $\lambda_{\text{med}}$) for 50 species. The solid lines are expected 1 : 1 relationships between the population growth rates if $\log \lambda_{\text{mean}}$ and the stochastic $\lambda$s were exactly equivalent. Each row represents a different stochastic population growth rate (a & b $\lambda_{\text{seq}}$, c & d $\lambda_{\text{Tulija}}$, e & f $\lambda_{\text{med}}$), the first column uses different symbols for common and rare species (a, c, e) and the second column uses different symbols for matrix dimensions (small, medium & large) (b, d, f).
of common or rare status; 51% of populations had positive population growth rates at the beginning of a study period but this reduced to 42% by the end of the study period. We offer four possible explanations for this overall negative trend in population growth rates, two of which reflect sampling artefacts and two of which reflect actual declines in abundance. The most obvious artefactual explanation would be if the sampling process itself caused deterioration of the vital rates determining population growth rate. We think this is unlikely for studies of plant demography because these typically involve minimal handling (few days per year). Second, demographers may tend to start studies in ‘best’ sites with relatively high population densities, increasing the likelihood of population declines. For example, Bierzychudek (1999) identified density-dependent population dynamics as a potential source of an unpredicted population decline. However, in our dataset increasing and decreasing populations were both equally likely at the beginning of a time period (100 populations log \( \lambda_{\text{mean}} > 0 \) and 97 populations log \( \lambda_{\text{mean}} < 0 \)), which is what we would expect from a random sample of populations with stable dynamics (log \( \lambda_{\text{mean}} = 0 \)).

Therefore, we suggest that this general pattern reflects more subtle causal factors. Researchers may choose to terminate studies after a particularly bad year or run of years leading to estimated declines in population growth rate. Finally, it may be that habitat quality itself tends to fluctuate over time. Fluctuating environmental conditions could reflect successional dynamics (Menges 1990) or changes in microbial communities, e.g. accumulation of pathogens or less beneficial mychorrizae (Bever 1994). If demographers tend to start studies in ‘best’ sites with relatively high population densities, then trends over relatively short time periods would be biased toward declines. If this mechanism were true, it would be necessary to establish study plots or transects not only in the central parts of the populations but also at the edges (i.e. sparser locations) that might be those ‘best’ locations in the future, to detect true population-level trends. Further study of the characteristics and locations of the studied populations may be able to tease out broad landscape scale patterns correlated with declining population growth rates (e.g. particular land-use types or habitats). If sampling bias causes an overly pessimistic view of population persistence, efficient and effective conservation and restoration actions may be compromised as, in the worst case, unnecessary management will be implemented.

Sources of variation in plant population growth rates

Quantifying variation in plant population dynamics across spatial and temporal scales is important for predictions of species abundance and distribution. Our comparative study based on a large number of plant species across different habitats revealed quantitative and qualitative differences between spatial and temporal variation in plant population dynamics. Population growth rates varied more between years than between populations, although the analysis of populations > 1 km apart reduced the difference between spatial and temporal variation, showing that greater temporal variation in plant populations is partly scale-dependent and caused by closely situated study populations within species. Earlier studies have detected synchronized population dynamics for short-lived grassland species (populations situated within a few kilometers), with the magnitude of synchrony clearly decreasing with increasing spatial distance among populations (e.g. Ramula et al. 2008b; Kiviniemi & Lofgren 2009). Our results suggest that synchronized population dynamics might occur also for longer-lived perennials, for instance, due to similar environmental factors in closely situated populations. Unfortunately, the level of detail on spatial locations reported was not adequate for us to construct a spatial variance–covariance matrix to further explore how distance between populations affects population growth rate and this remains a question for future studies.

Observed temporal variation in population growth rates was mainly due to variation in post-seedling survival regardless of the life-form; a typical pattern for long-lived perennials (Silvertown et al. 1993, 1996; de Kroon et al. 2000; Ramula et al. 2008a; Burns et al. 2010). In our case, we
cannot exclude the possibility that variation in plant growth is related to variation in population growth rate because variance in survival and growth were correlated. As expected, some of the variation in population growth rates was also explained by fire and herbivory because both these environmental factors can dramatically alter population dynamics over a short period of time. Although the effect of herbivory on plant population dynamics also depends on the timing of herbivory and the sensitivity of population growth rate to the life stages attacked (e.g. Ehrén 2002; Maron & Crone 2006; Ramula 2008), our findings suggest that both fire and herbivory influenced plant population dynamics largely through changes in plant survival as temporal changes in fecundity explained little variation in population growth rates.

Interestingly, population growth rates within populations were negatively temporally autocorrelated, meaning that good years were followed by bad years and vice versa. Although both variation in survival and fecundity explained negative autocorrelation in population growth rate, only variation in survival contributed to temporal variation in population growth rate. This indicates that fluctuating survival was the main driver of variation and temporal autocorrelation in plant population growth rates. Negative temporal autocorrelation driven by survival may be related to external (e.g. fire, herbivores) or internal (e.g. costs of reproduction) factors that modify survival directly or through correlations with the other vital rates.

Most stochastic population models assume that variation is uncorrelated in time (Menges 2000; Picó & Riba 2002; Kwit et al. 2004). However, a handful of studies point to the potential importance of temporally autocorrelated stochasticity (recently reviewed by Ruokolainen et al. 2009). These studies have most often argued for positive autocorrelations in population growth rates, due to resource storage, or slower changes in the physical or biological environment that buffer annual variation in environmental conditions (Halley 1996; Sabo & Post 2008). In contrast to both of these expectations, we observed negatively autocorrelated population growth rates. Negative temporal autocorrelation tends to dampen environmental stochasticity, and slows down extinction, resulting in a smaller extinction risk than positive temporal autocorrelation or pure ‘white noise’. However, in our dataset, realized population growth rates for ordered environments were more often lower than expectations without autocorrelations particularly for rare species with large negative autocorrelations (Fig. 7). Therefore, the temporal structure of variation in plant population dynamics needs more attention in future research.

Although our dataset of 50 perennials is just a sample of plant species and reflects any bias in the selection of species for demographic studies, it includes species from temperate ecosystems to the tropics and we therefore believe the dataset allows generalizations to be made about plant population dynamics. For instance, we can expect temporal variation in survival rather than temporal variation in fecundity to shape population dynamics of perennials, and we can expect population growth rates to be temporally autocorrelated. Departures from these generalizations may occur for special cases, such as invasive species, although we had insufficient invasive species to examine this in detail here but see Ramula et al. (2008a). We encourage demographers to continue conducting demographic studies, and to report detailed spatial and temporal information on their study populations and environmental factors to enable future comparative studies on plant population dynamics to seek explanations for how populations respond to their respective environments.

Consequences of realized temporal variation for plant populations

Deterministic population growth rates calculated from mean matrices were generally good predictors of stochastic population growth rates for randomly fluctuating environments, as others have also found (Boyce et al. 2006). However, the inclusion of observed temporal autocorrelation in population dynamics increased the difference between deterministic and stochastic population growth rates, and these differences were somewhat greater for rare species and species with small to medium matrix dimensions, where mean matrices usually produced more optimistic estimates of population performance than the stochastic methods. For our dataset, populations of rare species with small sample sizes (e.g. 60–200 individuals for Arabis fecunda, Astragalus satroides, Chamaecrista keyensis) were often responsible for the greatest differences between deterministic and stochastic population growth rates, suggesting that the greater difference for rare species is mainly because of larger sampling error. Larger sampling error resulted from small sample sizes (< 300 individuals) can lead to biased estimates of population growth rates derived from matrix population models (Ramula et al. 2009). Differences between deterministic and stochastic population growth rates for autocorrelated environments are important from a management point of view because small differences in annual $\lambda$ estimates accumulate over time, resulting in considerably different estimates of future population size.

Lessons from variation in plant population dynamics

Our synthesis of population growth rates for perennial plants has yielded important implications for understanding and predicting plant population dynamics, showing that environmental factors (e.g. fire and herbivory) strongly
influence population dynamics through space and time. The lack of a phylogenetic signal on patterns of population growth rates indicates that population dynamics can vary greatly from species to species even within the same genus. This makes it difficult to use demographic data from close relatives (e.g. congeners) as a surrogate to produce management recommendations when data for the target species are lacking. The use of demographic data from different populations within the same species would be more appropriate, particularly if geographic distances among populations are small and environmental factors similar. However, simple space-for-time substitutions in plant demographic analyses should be avoided. Greater temporal variation than spatial variation in population growth rates suggests that space-for-time data substitutions would underestimate the true variation in population growth rates, resulting in underestimated risk of extinction for declining populations and consequently, over-optimistic predictions of species performances.

Our results show that post-seedling survival is the key vital rate contributing to temporal variation in population growth rate and driving temporal autocorrelation of annual population growth rates for perennial plants. Temporal autocorrelation in population growth rates can rarely be ignored in predictions of population dynamics as it occurs in many plant populations and can change estimates of the long-term population growth rate. For randomly fluctuating environments realized variation in vital rates has a small effect on plant population dynamics and mean matrix and stochastic population growth rates are highly correlated, although stochastic growth rates tend to be lower. However, for temporally autocorrelated environments variation in vital rates results in a slightly greater difference between mean matrix and stochastic population growth rates. For species with strong positive or negative autocorrelations, stochastic population growth rates for temporally autocorrelated environments differed from those for randomly fluctuating environments. This indicates that the sequence of environmental conditions is essential for determining plant population growth rate and should therefore be incorporated into predictions of population dynamics. Temporal autocorrelation in population dynamics necessitates long-term observations over several years to produce estimates of population performance, a finding that will be particularly important in the face of future environmental change.

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REFERENCES


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Ramula, S., Rees, M. & Buckley, Y.M. (2009). Integral projection models perform better for small demographic data sets than...


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Phylogeny for 49 plant species used for deterministic analyses.

**Figure S2** Fitted population growth rates for all populations of 49 plant species.

**Table S1** Species included in the database.

**Table S2** Model comparison with and without phylogeny for log \( \lambda_{det} \).

**Table S3** Parameter estimates for models of log \( \lambda_{det} \) and \( \sigma \log \lambda_{det} \).

**Table S4** Species with environmental factors.

**Table S5** Herbivory levels for four species.

**Table S6** Parameter estimates for the effect of temporal autocorrelation on \( \lambda_{seq} \).

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