LETTER

A life-history perspective on the demographic drivers of structured population dynamics in changing environments

David N. Koons[1]* David T. Iles[1]
Michael Schaub[2] and Hal Caswell[3]

Abstract

Current understanding of life-history evolution and how demographic parameters contribute to population dynamics across species is largely based on assumptions of either constant environments or stationary environmental variation. Meanwhile, species are faced with non-stationary environmental conditions (changing mean, variance, or both) created by climate and landscape change. To close the gap between contemporary reality and demographic theory, we develop a set of transient life table response experiments (LTREs) for decomposing realised population growth rates into contributions from specific vital rates and components of population structure. Using transient LTREs in a theoretical framework, we reveal that established concepts in population biology will require revision because of reliance on approaches that do not address the influence of unstable population structure on population growth and mean fitness. Going forward, transient LTREs will enhance understanding of demography and improve the explanatory power of models used to understand ecological and evolutionary dynamics.

Keywords

Age structure, global change, life history, matrix model, non-stationary, perturbation analysis, stage structure, stochasticity, transient dynamics, vital rate.

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INTRODUCTION

Population growth rates are central to ecology and evolution. Not only do they describe changes in species abundance within a given area, they also quantify mean fitness for a population of individuals sharing a particular gene or life-history strategy (Fisher 1930), the ability of a rare mutant to invade a more common established type (Metz *et al.* 1992), or the ability of rare species to invade communities of more common residents (Chesson 2000). Not surprisingly, a major goal of ecology and evolution is to understand the demographic mechanisms that drive population growth and affect fitness (Coulson *et al.* 2006).

For example, quantitative geneticists strive to understand the relative influence of viability (i.e. survival) and reproductive selection on trait change over time, as moderated by heritability (Lande 1982). Others study life-history evolution by comparing the demographic drivers of population dynamics across species along an evolved phylogeny (Sæther & Bakke 2000). Population ecologists use similar approaches to design more effective conservation and management strategies (Caswell 2000), and to develop mechanistic projections of population dynamics (e.g. Jenouvrier *et al.* 2014). Community biologists have even found that the processes controlling species coexistence and biodiversity can be better understood by identifying the specific demographic parameters that contribute most to the outcomes of competition (Adler *et al.* 2010).

Prospective perturbation analyses predict the change in demographic outcomes that would result from any specified change in the parameters that determine those outcomes, whereas retrospective perturbation analyses, such as life table response experiments (LTRE), aim to decompose the effects of realised change in parameters on past demographic outcomes (Caswell 2000). LTREs were first developed (Caswell 1989), and are most often used to decompose effects on asymptotic growth rates from deterministic models, but also have been applied to net reproductive rates, invasion wave speeds, operational sex ratios, stochastic growth rates, periodic growth rates, life expectancy and measures of lifespan inequality (Caswell 2010). Our goal here is to develop and apply LTRE analysis to a particular class of short-term transient population growth rates in variable environments.

Although common analyses of the stochastic growth rate incorporate the effects of fluctuating vital rates and population structure in variable environments, they rely on the stochastic environment being stationary (e.g. Tuljapurkar 1990). Many contemporary environments, however, are not stationary. For example, changes in climate, land-use, and water-use are directional, creating 'non-stationary' environments for much of the world's biota (Wolkovich *et al.* 2014).

Non-stationary environments keep populations in a perpetual transient state because they never have a chance to converge to a stable population structure (Hastings 2004; Wolkovich *et al.* 2014). Recent studies of transient dynamics have produced measures of the amplification of isolated perturbations (e.g. Neubert & Caswell 1997; Verdy & Caswell 2008; Stott *et al.* 2011; Iles *et al.* 2016) and general methods for the sensitivity analysis of transient dynamics (Caswell

[1]*Department of Wildland Resources and the Ecology Center, Utah State University, 5230 Old Main Hill, Logan, UT 84322-5230, USA*

[2]*Swiss Ornithological Institute, Sempach 6204, Switzerland*

[3]*Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, 1090 GE, The Netherlands*

Correspondence: E-mail: david.koons@usu.edu

2007; Caswell & Sánchez Gassen 2015), but retrospective analyses of transient dynamics have yet to be developed.

To improve our understanding of structured population dynamics in changing environments, we present a series of LTRE analyses that decompose transient population growth rates into contributions from vital rates and population structure in any type of time-variant environment (stochasticity is one case, but others include trends, periodicity and regime shifts). Although it is a slight misnomer because there are many other possibilities for LTRE analysis of transient population dynamics, for simplicity we will call these 'transient LTREs'. We then implement our transient LTREs in a theoretical framework inspired by the demographic buffering hypothesis, which predicts that because of the deleterious impact temporal variability in vital rates can have on fitness, such variability should decrease with increasing elasticity of population growth rate to the vital rate in question (e.g. Gaillard & Yoccoz 2003). Corresponding to this prediction, inverse relationships between prospective elasticities and retrospective vital rate contributions to variation in population growth rates have been found in birds (Sæther & Bakke 2000; Koons *et al.* 2014), large mammals (Gaillard *et al.* 2000), and some plants (Zuidema *et al.* 2007), presumably because natural selection has buffered vital rates with the greatest potential to affect fitness against environmental variation.

The aforementioned patterns were nevertheless based on analyses of asymptotic population growth rates associated with long-term stability of population structure. Using transient LTRE analyses, we relax the need for such applications and reveal gaps in our current understanding of the relationship between life-history and population dynamics that will need revision when near-term inference is desired in time-varying environments. In addition, we discuss how our transient LTREs can be applied to an array of other problems in ecology and conservation.

THE POPULATION MODEL AND DEMOGRAPHIC OUTCOMES

Throughout, we use the time-variant population model,

$$\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t \tag{1}$$

where $\mathbf{n}_t$ is a vector containing j components of structured abundance n, and $\mathbf{A}_t$ is a projection matrix containing the vital rates at time t. With a focus on time-varying environments, LTRE analysis has been used to decompose vital rate contributions to sequential changes in asymptotic growth rates (λ_1) associated with each $\mathbf{A}_t$ (e.g. Oli & Armitage 2004), and more commonly, the variance of λ_1 over time (reviewed by Bassar *et al.* 2010). But, a focus on λ_1 obscures the manner in which structured abundance $\mathbf{n}_t$ acts on $\mathbf{A}_t$ (see eqn 1) to determine realised rates of growth in time-varying environments:

$$\lambda_{\text{realised},t} = \frac{\sum_j n_{j,t+1}}{\sum_j n_{j,t}} = \frac{N_{t+1}}{N_t} = \frac{||\mathbf{A}_t \mathbf{n}_t||}{||\mathbf{n}_t||} \tag{2}$$

where $|| \ ||$ denotes the sum of (absolute value) entries in a vector. More recently, LTRE analysis has been extended to the

stochastic growth rate, defined as the long-run average of logged $\lambda_{\text{realised},t}$:

$$\log \lambda_s = \lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \log \lambda_{\text{realised},t} \tag{3}$$

which embraces the dynamic feedback between $\mathbf{n}_t$ and $\mathbf{A}_t$ in a time-varying environment (Caswell 2010; Davison *et al.* 2010). Existence of an asymptotic limit for $\log \lambda_s$, however, depends on the stochastic environment being stationary so that population structure eventually has a stable mean and variance (Cohen 1979).

In the near-term and in non-stationary environments, transient demographic outcomes will be of greater interest. For example, following a management intervention or environmental perturbation of particular interest, one might be interested in the change in $\lambda_{\text{realised},t}$ between successive time steps, locations, or phenotypes ($\Delta \lambda_{\text{realised}}$). Temporal variability of $\lambda_{\text{realised},t}$, $\text{var}(\lambda_{\text{realised},t})$, is also of concern because occurrences of $\lambda_{\text{realised},t} \ll 1$ and $\lambda_{\text{realised},t} \gg 1$ lead to large declines and spikes in N_{t+1} that can, respectively, predispose populations to extinction or create problems for sustainable management. In such cases, decomposing change or variance in $\lambda_{\text{realised},t}$, not λ_1 (Fig. 1A–D), will reveal which demographic pathways contribute most to actual change or variance in near-term fitness and population growth (Coulson *et al.* 2005).

The impact of non-stationary environmental change on the mean rate of population growth over time is also of concern in ecology and conservation (Gotelli & Ellison 2006), as well as microevolutionary studies that seek to understand the drivers of change in mean fitness between one generation and the next (Lande 2007). The average rate of population growth over a short to moderate time period T is measured as the geometric mean of $\lambda_{\text{realised},t}$ (see Fig. 1E):

$$\lambda_g = \left(\prod_{t=0}^{T-1} \lambda_{\text{realised},t} \right)^{1/T}, \ \log \lambda_g = \frac{1}{T} \sum_{t=0}^{T-1} \log \lambda_{\text{realised},t} \tag{4}$$

In non-stationary environments, $\log \lambda_g$ is transient and different than $\log \lambda_s$ because of perpetual instability in population structure that never approaches a stationary distribution (see Hunter *et al.* 2010 for an application).

TRANSIENT LTRES FOR TIME-VARYING ENVIRONMENTS

We now develop LTRE analyses for each of the transient demographic outcomes described above. To decompose past $\text{var}(\lambda_{\text{realised},t})$, we use methods derived from the definition of variance for a linear combination of variables (e.g. Caswell 2001 ch. 10). Without affecting the measurement of $\lambda_{\text{realised},t}$, we normalise all $\mathbf{n}_t$ to sum to one in order to avoid issues with numerical computation (denoted $\hat{\mathbf{n}}_t$). We then place each parameter comprising the elements of $\mathbf{A}_t$ (i.e. lower level vital rates) and each component of $\hat{\mathbf{n}}_t$ into a vector $\mathbf{\Theta}_t$, and calculate the sensitivity of $\lambda_{\text{realised},t}$ to change in each underlying demographic parameter ($\partial \lambda_{\text{realised},t} / \partial \theta_{i,t}$) using either symbolic (see Appendix S1) or matrix calculus (see Caswell 2007). These sensitivities are then used along with covariance among
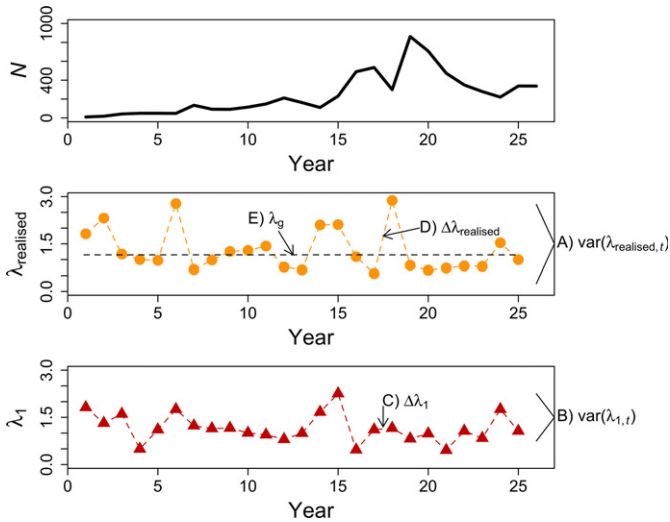
Figure 1 A roadmap to demographic outcomes in the paper. In the top panel is a trajectory of abundance for an example life history described by eqn 9 with $\overline{S_J} = 0.15$, $\overline{S_A} = 0.85$, $\overline{\rho}$ suitable for population growth (4.03), and $\gamma = 0.5$ in a medium variance environment, the associated rates of realised population growth between each time step ($\lambda_{\mathrm{realised},t}$, middle panel), and the very different asymptotic growth rates associated with the vital rates at each time step ($\lambda_{1,t}$, bottom panel). To retrospectively decompose the dynamics of this focal population, one could use the transient LTRE from eqn 6 to measure the direct contributions of vital rates and components of population structure to the variance of $\lambda_{\mathrm{realised},t}$ over time (A) instead of the often-used LTRE analysis of vital rate contributions to the variance of asymptotic $\lambda_{1,t}$ (B). Past researchers have also examined the contributions of vital rates to sequential changes in $\lambda_{1,t}$ over time ($\Delta\lambda_1$, C). By not accounting for the interplay between population structure and vital rates, however, analyses of $\lambda_{1,t}$ do not capture the correct magnitude of change in abundance, and may even analyse the wrong direction of change (e.g. compare C to D). Instead, one can now use eqn S1.4 to examine the contributions of each demographic parameter to change in $\lambda_{\mathrm{realised},t}$ at particular points in time ($\Delta\lambda_{\mathrm{realised}}$, D). One can also decompose the drivers of difference in the geometric average of growth rates ($\lambda_g = 1.16$) between one period of time (as shown in E) and either a prior or subsequent time period of equal duration (eqn 8).

all elements of $\boldsymbol{\Theta}_t$ to obtain the first-order approximation of variation in $\lambda_{\mathrm{realised},t}$,

$$\mathrm{var}(\lambda_{\mathrm{realised},t}) \approx \sum_i \sum_j \mathrm{cov}(\theta_{i,t}, \theta_{j,t}) \frac{\partial \lambda_{\mathrm{realised},t}}{\partial \theta_{i,t}} \frac{\partial \lambda_{\mathrm{realised},t}}{\partial \theta_{j,t}} \bigg|_{\overline{\theta_{ij}}} \quad (5)$$

where the sensitivities are evaluated at the mean of $\boldsymbol{\Theta}_t$ across a realised (or simulated) time series. Each term in eqn 5 is the contribution to variance in $\lambda_{\mathrm{realised},t}$ from the covariance among each pair of parameters (which includes population structure and vital rates). A measure of the contribution of variation in each θ_i to $\mathrm{var}(\lambda_{\mathrm{realised},t})$ is obtained by summing over the covariances (Horvitz *et al.* 1997):

$$\chi_{\theta_i} \approx \sum_j \mathrm{cov}(\theta_{i,t}, \theta_{j,t}) \frac{\partial \lambda_{\mathrm{realised},t}}{\partial \theta_{i,t}} \frac{\partial \lambda_{\mathrm{realised},t}}{\partial \theta_{j,t}} \bigg|_{\overline{\theta_{ij}}} \quad (6)$$

The magnitude of χ_{θ_i} may be small because $\lambda_{\mathrm{realised},t}$ is insensitive to changes in $\theta_{i,t}$, because θ_i exhibits little variability over time, or because negative co-variation with other θ_j nullifies its direct effect. The transient LTRE decomposition of $\mathrm{var}(\lambda_{\mathrm{realised},t})$ in eqns 5 and 6 is different from traditional

LTRE analysis of asymptotic growth rates (λ_1) associated with the matrices $\mathbf{A}_t$ in that it analyses the actual transient growth, $\lambda_{\mathrm{realised},t}$, occurring from t to $t + 1$. A transient analysis reveals how strongly fluctuations in population growth rate have been driven by the direct effects of each vital rate, each component of population structure, and sums of χ_{θ_i} across parameters of interest. The transient LTRE decomposition of $\Delta\lambda_{\mathrm{realised}}$ is extremely similar to that for $\mathrm{var}(\lambda_{\mathrm{realised},t})$ in eqns 5 and 6, and thus we provide it in Appendix S1.

To develop an LTRE decomposition of demographic contributions to the difference in mean population growth rates between one period of time (1) and another (2), $\log \lambda_g^{(2)} - \log \lambda_g^{(1)} = \Delta \log \lambda_g$, we adopted a format similar to eqn 1 in Davison *et al.* (2010) for LTRE analysis of $\log \lambda_s$. Like the difference in $\log \lambda_s$ between populations, transient $\Delta \log \lambda_g$ between two periods of time for a single population depends on change in the temporal mean and standard deviation of each vital rate between time periods, and potentially changes in higher statistical moments (not considered here, but see the discussion). As in any LTRE analysis, the contribution of realised change in these vital rate moments to $\Delta \log \lambda_g$ will also depend on the sensitivity of the time-averaged growth rate to proportional perturbations in the vital rate moments (i.e. elasticities, which are used instead of unit perturbations because of working on the log scale).

Different from elasticities for the long-term stochastic growth rate, those for λ_g must account for non-stationary population structure, which can be attained using the 'real-time elasticities' developed by Haridas *et al.* (2009). These include $e_{i,t}^{\mathbf{A}}$, the real-time elasticity of $\lambda_{\mathrm{realised},t}$ to perturbation in vital rate i at time t while holding population structure fixed at realised values, and of key importance, $e_i^{\hat{\mathbf{n}}_t}$, the elasticity of $\lambda_{\mathrm{realised},t}$ to change in population structure at time t resulting from perturbations to vital rate i at all previous time steps. The perturbations can be implemented in ways that change the temporal mean (μ) of a vital rate or its standard deviation (σ). By iterating the calculations for $e_{i,t}^{\mathbf{A}}$ and $e_i^{\hat{\mathbf{n}}_t}$ across all t in time period T and taking the finite limit, one attains $e_i^{\mathbf{A}}$ and $e_i^{\hat{\mathbf{n}}}$ (t sub- and super-scripts have been dropped), which respectively represent the elasticity of λ_g to change in vital rate i while ignoring the effect of perturbations on population structure, and that to change in population structure while ignoring the direct effect of perturbations in vital rate i. Although $e_i^{\mathbf{A}}$ and $e_i^{\hat{\mathbf{n}}}$ converge asymptotically to elasticities of the long-term stochastic growth rate in a stationary environment, they can be notably different when population structure is not stationary (Fig. 1 in Haridas *et al.* 2009; Haridas & Gerber 2010). By evaluating the aforementioned elasticities for a reference population defined by per time step means of $\Theta_t^{(1)}$ and $\Theta_t^{(2)}$ (where time periods 1 and 2 are of equal duration; see Appendix S1), the LTRE for transient $\Delta \log \lambda_g$ can be approximated as:

$$\Delta \log \lambda_g \approx \sum_i \left(\log \mu_i^{(2)} - \log \mu_i^{(1)} \right) \left(e_{\mu_i}^{\mathbf{A}} + e_{\mu_i}^{\hat{\mathbf{n}}} \right)$$
$$+ \sum_i \left(\log \sigma_i^{(2)} - \log \sigma_i^{(1)} \right) \left(e_{\sigma_i}^{\mathbf{A}} + e_{\sigma_i}^{\hat{\mathbf{n}}} \right) \quad (7)$$

where μ_i denotes the mean of vital rate i over a given time period and σ_i the standard deviation describing temporal

variability. The total contribution of vital rate i to transient $\Delta \log \lambda_g$ can thus be represented as a function of four unique contributions:

(1) the direct effect of a difference between $\mu_i^{(2)}$ and $\mu_i^{(1)}$,
(2) the indirect effect of $\mu_i^{(2)} - \mu_i^{(1)}$ channelled through population structure,
(3) the direct effect of a difference between $\sigma_i^{(2)}$ and $\sigma_i^{(1)}$, and
(4) the indirect effect of $\sigma_i^{(2)} - \sigma_i^{(1)}$ channelled through perturbed population structure, which collectively appear as:

$$\chi_{\theta_i} \approx \Delta \log \mu_i \times e_{\mu_i}^{\mathbf{A}} + \Delta \log \mu_i \times e_{\mu_i}^{\hat{\mathbf{n}}} + \Delta \log \sigma_i \times e_{\sigma_i}^{\mathbf{A}} + \Delta \log \sigma_i \times e_{\sigma_i}^{\hat{\mathbf{n}}} \tag{8}$$

Additional information about the steps for implementing eqns 5–8 is provided in Appendix S1, and pseudo code with annotated R code is provided in Appendix S2.

COMPARISON OF LTRES ACROSS LIFE HISTORIES

To compare the inference attained from LTRE analyses across life-history strategies, we simulated life histories in time-varying environments using a version of the simple two-stage matrix population model presented in Neubert & Caswell (2000),

$$\mathbf{A}_t = \begin{bmatrix} S_{J,t}(1-\gamma) & \rho_t \\ S_{J,t}\gamma & S_{A,t} \end{bmatrix} \tag{9}$$

where S_t represents per time step survival for either juvenile (J) or adult (A) stage classes, γ denotes the fraction of surviving juveniles that mature to become adults during each time step, and ρ_t denotes time-specific recruitment of offspring into the juvenile stage (the number of juveniles at $t + 1$ produced by an adult at t; the lower level processes comprising ρ_t will differ widely among species). This versatile model can describe a wide array of life histories. For example, semelparity is approached as $S_{A,t} \to 0$, and iteroparity increases as $S_{A,t} \to 1$. Likewise, delayed development is enhanced as γ approaches (but is not allowed to reach) 0, and a precocial life history is attained as $\gamma \to 1$ (Neubert & Caswell 2000).

Comparative LTRE analyses of variability in population growth rates

We next sought to examine transient LTRE contributions of vital rates and components of population structure to temporal variation in $\lambda_{\text{realised},t}$ (eqn 6) across a wide array of life-history strategies, and for heuristic purposes, to compare results from this method to those produced by a traditional LTRE analysis of variance in asymptotic growth rates (λ_1) associated with each $\mathbf{A}_t$ (such calculations necessarily ignore the effects of population structure). To denote vital rate values in mean environmental conditions, we used eqn 9 to generate life histories by creating a grid of all possible combinations of $\overline{S_J}$ and $\overline{S_A}$, with each ranging from 0.05 to 0.95 (in steps of 0.05). We fixed γ at either 0.2, 0.5 or 0.8, and solved for $\overline{\rho}$ such that each life history had asymptotic $\lambda_1 = 1$ in mean environmental conditions. To allow for reasonable comparison with the

asymptotic LTRE, we generated stationary temporal variation in $S_{J,t}$, $S_{A,t}$ and ρ_t for each life history in a manner that was consistent with the demographic buffering hypothesis. To do so, we measured the elasticities of λ_1 for each life history to proportional change in $\overline{S_J}$, $\overline{S_A}$, and $\overline{\rho}$, one at a time, denoted as e_i. Next, we scaled the simulated temporal variance in $S_{J,t}$, $S_{A,t}$ and ρ_t by defining a proportional measure of buffering: $\tau_i = (1 - e_i)/\max(e_{S_J}, e_{S_A}, e_\rho)$, using the fact that all e_i were < 1 for our simulated life histories. Thus, τ_i is smallest (and most buffered) for the vital rate with largest elasticity and vice versa. For each vital rate, we simulated low ($\tau_i \times 0.25 \times \text{CV}_{\max}$), medium ($\tau_i \times 0.50 \times \text{CV}_{\max}$) and high temporal variance scenarios ($\tau_i \times 0.75 \times \text{CV}_{\max}$), where $\text{CV}_{\max}$ pertains to the maximum possible coefficient of variation for a probability (Morris & Doak 2004) or a set value of one for ρ_t. To test whether our results were dependent on these choices, we also considered scenarios with $\tau_i = 1$ for each vital rate, which implies no demographic buffering.

After generating random values of $S_{J,t}$ and $S_{A,t}$ from independent beta distributions, and random values of ρ_t from a gamma distribution for each life history, we projected population dynamics for 25 time steps using eqn 1; a length of time that could be considered not only as a long-term ecological study (Clutton-Brock & Sheldon 2010) but also one where the distribution of population structure could not have had enough time to converge to its stationary distribution. To be consistent across life histories and conservative in our comparisons to asymptotic LTRE analyses of temporal variance in λ_1, we set initial conditions for each projection ($\mathbf{n}_0$) to the stable stage distribution associated with respective values of $S_{J,t}$, $S_{A,t}$, γ and ρ_t at the initial time step for each life history. For all projections, we measured the transient LTRE contributions of variation in each θ_i to $\text{var}(\lambda_{\text{realised},t})$ across the duration of each 25 time step simulation using eqn 6. We also measured the asymptotic LTRE contributions of each vital rate to $\text{var}(\lambda_1)$, and measured any approximation errors in $\sum_i \chi_{\theta_i}$ associated with each LTRE relative to actual $\text{var}(\lambda_{\text{realised},t})$. We note that although the LTRE analysis of asymptotic λ_1 is not designed to examine $\text{var}(\lambda_{\text{realised},t})$, many apply it in hopes of approximating the demographic parameters that contribute most to realised fluctuations in growth rates of wild populations (Bassar *et al.* 2010). Thus, we feel that our measure of approximation error described above will help direct future research to the LTRE that is most appropriate to the objective.

Results

Because of strong qualitative similarity in the results across simulated levels of maturation probability (γ) and environmental variance, we focus primarily on those pertaining to life histories with $\gamma = 0.5$ and medium levels of variability in the vital rates that emulated demographic buffering (see Appendix S3 for results from other simulation scenarios and Appendix S4 for those that did not emulate demographic buffering, $\tau_i = 1$). Across life histories, we found that the contribution of population structure to $\text{var}(\lambda_{\text{realised},t})$ was greatest in those with low $\overline{S_J}$ and low $\overline{S_A}$ (e.g. nearly annual plants and invertebrates), which curtailed in a diagonal fashion across the array towards life histories with high $\overline{S_J}$ and $\overline{S_A}$ (e.g. large mammals) (Fig. 2A, Appendix S3.1). In fact,

fluctuations in population structure made the largest contribution to $\text{var}(\lambda_{\text{realised},t})$ in life histories with low to moderate $\overline{S_J}$ and low $\overline{S_A}$, but also across a larger range of $\overline{S_A}$ when $\overline{S_J}$ was at its lowest (Fig. 2B, Appendix S3.2). For many life histories with moderate longevity and parity (which pertains to many species), as well as the nearly semelparous life histories with low $\overline{S_A}$ but high $\overline{S_J}$ (e.g. cicadas), fluctuations in offspring recruitment (ρ_t) made the largest contribution to $\text{var}(\lambda_{\text{realised},t})$. To the contrary, fluctuations in either juvenile or adult survival made the largest contribution in some long-lived and highly iteroparous life histories (upper right corners in Fig. 2B, Appendix S3.2). These life-history patterns were even more marked in the life histories without demographic buffering (Appendix S4.1B), indicating that the patterns are not unique to the demographic buffering hypothesis.

Corresponding results from asymptotic LTRE analyses of λ_1 were markedly different than those presented above for transient LTRE analyses of $\lambda_{\text{realised},t}$ (Fig. 2C, Appendices S3.3, S4.1C), indicating the asymptotic LTRE may provide poor insight into the drivers of actual population growth rates in time-varying environments. The mean ratio of approximation error on the log scale, $\log\left(\text{var}(\lambda_{\text{realised},t}) \middle/ \sum_i \chi_{\theta_i,t}\right)$, across all life histories was indeed high, increased with environmental variability (0.75, 0.86 and 0.95 in the low, medium and high variance scenarios relative to an error-free value of 0), and the bias was consistently in the direction where $\sum_i \chi_{\theta_i}$ was low compared to $\text{var}(\lambda_{\text{realised},t})$. This indicates that the analysis of asymptotic growth rates does not fully capture the magnitude of variance in realised growth rates. Moreover, there were distinct life-history patterns in the error, which tended to be strongest in life histories where fluctuating population structure made large contributions to actual $\text{var}(\lambda_{\text{realised},t})$, as well as those with extremely low $\overline{S_J}$ and extremely high $\overline{S_A}$ (e.g. trees and long-lived vertebrates with indeterminate growth), for which fluctuating population structure made moderate contributions (Figs. 2A, 3A, Appendices S3.4, S4.2A). This is not surprising because the variance of λ_1 is by definition unaffected by fluctuating population structure, an important reminder that asymptotic LTRE analyses of λ_1 overlook these important effects that occur in time-variant environments.

The approximation error for transient LTREs across all life histories, on the other hand, was only 0.01, 0.04 and 0.06 in the low-, medium- and high-variance scenarios. The nominal levels of error were moreover distributed in a near-symmetric fashion in low and high directions across life histories (i.e. no life-history patterns in the error; Fig. 3B, Appendices S3.5, S4.2B). Thus, the transient LTRE provided accurate approximations of how vital rates and population structure contribute to $\text{var}(\lambda_{\text{realised},t})$ in time-variant environments.

Comparative LTRE analyses in non-stationary environments

Given that we have established transient LTREs as being more appropriate for decomposing variability of realised population growth rates in time-variant environments than commonly used asymptotic LTREs, we now turn attention to the comparison of transient LTREs across life histories in non-stationary
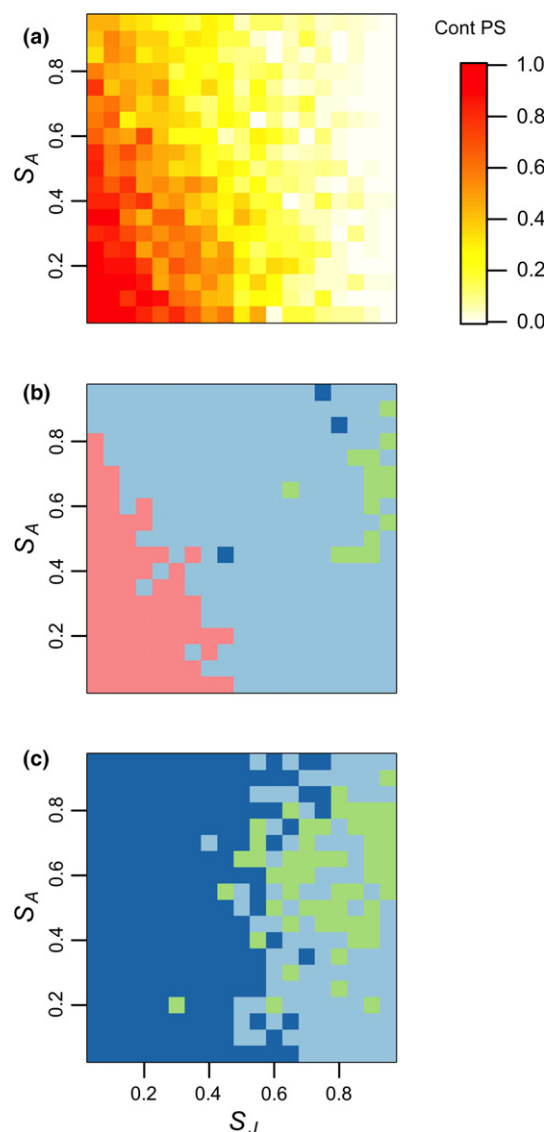

Figure 2 The proportional contribution of population structure (PS) to $\text{var}(\lambda_{\text{realised},t})$ in medium variance environments across life histories with $\gamma = 0.5$ according to the transient LTRE (eqn 6), for which the complement represents the proportional contribution from all vital rates combined (panel A). Also shown in panel B are the demographic parameters that contributed most to $\text{var}(\lambda_{\text{realised},t})$ across the same array of life histories (ρ_t = light blue, $S_{J,t}$ = dark blue, $S_{A,t}$ = light green, and $\hat{n}_{A,t}$ = salmon; $\hat{n}_{J,t}$ never made the largest contribution for any life history), which differed greatly from the vital rates that contributed most to $\text{var}(\lambda_1)$ according to the asymptotic LTRE (panel C).

environments. Because there are near-infinite ways in which demography can respond to non-stationary environmental change, it is difficult to study population dynamics in such environments from a theoretical angle. For example, all vital rates might respond to environmental change in the same direction, only a subset might respond, or vital rates might respond in opposite directions (e.g. because of trade-offs). In addition, non-stationary environmental change might affect the means of vital rates, their variances, or both, and a large array of other possibilities could occur (Wolkovich *et al.* 2014).
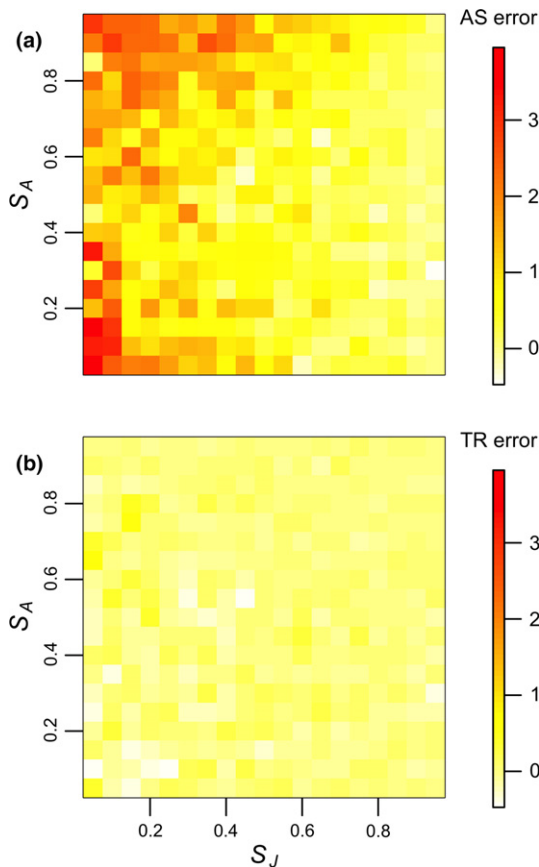
Figure 3 The approximation error in summed contributions of vital rates to var(λ_1) measured with asymptotic LTREs relative to variance in realised population growth rates: $\log\left(\text{var}(\lambda_{\text{obs},t})/\sum_i \chi_{\theta_i}\right)$ (AS; panel A), which exhibited much more error and distinctive life-history patterns in the error relative to the more appropriate transient LTRE method from eqn 6 (TR; panel B). Results are shown across life histories with $\gamma = 0.5$ in medium variance environments.

To provide just a few examples of how transient LTRE inference varies across life histories in non-stationary environments, we created a trend parameter (β_{VR}) for non-stationary change in ρ_t, $S_{J,t}$, or $S_{A,t}$ from eqn 9, one at a time:

$$\text{VR}_t = \text{link}^{-1}\left(a_{\text{VR}} + \beta_{\text{VR}} \times t + \varepsilon_{\text{VR},t}\right) \qquad (10)$$

where t was projected 25 time steps past the stationary simulations described in the sub-section above and mapped to the $U[0,1]$ space for multiplication with β_{VR} in eqn 10, a_{VR} forced the vital rate to have the same mean as in the stationary simulation when mapped $t = 0$ and $\varepsilon_{\text{VR},t} = 0$, and β_{VR} was chosen so that the mean would decline by 25% on the real parameter scale by the end of the projection. We simulated values of $\varepsilon_{\text{VR},t}$ using a normal distribution with a mean of zero and a variance that was 25% of that used in the stationary simulations because, in addition to $\varepsilon_{\text{VR},t}$, the β_{VR} trend also affects the net variance of a vital rate across non-stationary conditions. A logit link was used for survival probabilities and a log link was used for ρ_t. When not affected by the non-stationary process in eqn 10, we allowed the other vital rates to fluctuate in a stationary manner as described in the previous sub-section. We note that one could modify eqn 10 to affect

multiple vital rates at the same time, or accommodate trends in $\varepsilon_{\text{VR},t}$ instead of the central tendency. Nonlinear equations would be needed to model environmental shifts out of equilibrium conditions and bifurcations into alternative states.

Given our simple trend scenarios, we used a transient LTRE to measure the contributions of each demographic parameter to sequential changes in $\lambda_{\text{realised},t}$ (i.e. sequential $\Delta\lambda_{\text{realised}}$) over the duration of non-stationary simulations for life histories near each corner of our array (each with $\gamma = 0.5$; see Appendix S6). But below, we focus on vital rate contributions to the difference in log λ_g between periods of non-stationary change in each focal vital rate (ρ_t, $S_{J,t}$, or $S_{A,t}$) and the preceding stationary period using eqn 8.

Results

Similar to our findings for transient contributions of demographic parameters to var($\lambda_{\text{realised},t}$) in stationary environments, we found that the $\Delta\log \lambda_g$ resulting from non-stationary environmental change in life histories with low $\overline{S_J}$ (e.g. species that invest in offspring quantity rather than quality) was predominantly driven by indirect effects of vital rates channelled through perturbations to population structure ($\hat{\mathbf{n}}$; Fig. 4). These impacts were largely manifested through changes in the mean (μ) of offspring recruitment (Fig. 4 panel A) or juvenile survival (panel C).

As longevity and parity of the life history increased, however, the direct effect of vital rates (**A**) contributed more to $\Delta\log \lambda_g$ than the indirect effects. Moreover, the vital rate that experienced progressive non-stationary change in its mean over time tended to make the greatest contribution (compare bar clusters in Fig. S5), which often resulted in a greater vital rate contribution to $\Delta\log \lambda_g$ than that to var($\lambda_{\text{realised},t}$) in the stationary environments (Fig. 2). These patterns were especially pronounced in the life history with highest longevity and parity (Fig. 4 panel B), for which population dynamics can be particularly responsive to even small changes in adult survival.

In all life histories, the direct and indirect contributions of change in vital rate standard deviations to $\Delta\log \lambda_g$ were small (Fig. 4), but could have been greater had we focused on non-stationary changes in variability over time instead of the central tendency. Overall, the logged approximation errors associated with the transient LTRE for $\Delta\log \lambda_g$ were quite small in each of the non-stationary scenarios we considered (respectively -0.03, 0.09, 0.13; -0.01, 0.03, -0.02; 0.01, 0.24, -0.07; and 0.01, 0.06, 0.07 for life-history panels A-D in Fig. S5), but this will not necessarily be the case in all settings.

DISCUSSION

Despite the maturity of population biology, there is still much to be learned about the behaviour of population dynamics in changing environments. For example, comparative studies of demography have inspired multiple disciplines, ranging from the study of trait evolution (e.g. Adler *et al.* 2014) to directing conservation and management of poorly studied species based on demographic life-history patterns (e.g. Sæther & Bakke 2000). Until recently, however, the most commonly used tools for retrospectively examining ecological and evolutionary dynamics have been based on asymptotic growth rates (Bassar
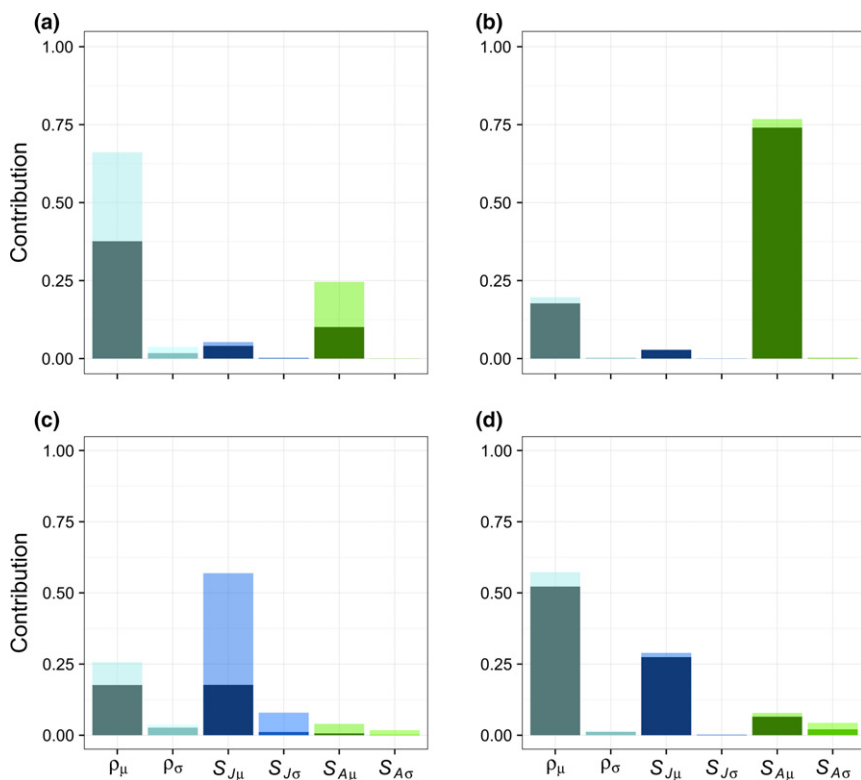
Figure 4 The relative contribution (y-axis: $\mathrm{abs}(\chi_{\theta_{i,x}})\big/\sum_i\sum_x \mathrm{abs}(\chi_{\theta_{i,x}})$) of each vital rate (x-axis: θ_i) to the difference in log λ_g between the time period with non-stationary environmental change in $S_{A,t}$ and the preceding period with stationary variability, partitioned according to four effects (x): the direct effect (dark shading at bottom of stacked bars) of change in the mean (μ) or standard deviation (σ) of a vital rate, or the respective indirect effects channelled through perturbed population structure (light shading at top of stacked bars). Panels A, B, C and D, respectively, represent the life histories near each corner of our array with $\overline{S_A} = 0.85$ and $\overline{S_J} = 0.15$, $\overline{S_A} = 0.85$ and $\overline{S_J} = 0.85$, $\overline{S_A} = 0.15$ and $\overline{S_J} = 0.15$, and $\overline{S_A} = 0.15$ and $\overline{S_J} = 0.85$. See Appendix S5 for results pertaining to non-stationary change in each of the other vital rates.

et al. 2010). Our transient LTREs overcome the need for such applications, and can be used to measure the dual contributions of vital rates and population structure to population dynamics in the observed environments.

By implementing transient LTREs across a wide array of simulated life histories, we have provided a 'tree of life' perspective into the demographic drivers of population dynamics in time-variant environments, and identified where current knowledge may be incorrect because of reliance on applications that were not meant for such conditions. Consistent with comparative studies of prospective population dynamics in time-varying environments (Gamelon *et al.* 2015), our results would suggest that it is most critical to account for fluctuating population structure when analysing population dynamics and evolutionary processes of the many species that do not possess the luxury of extremely high adult survival. Unstable population structure has the potential to strongly affect population dynamics in long-lived species (Koons *et al.* 2005, 2006), but negative co-variation with the vital rates tends to nullify its impact in a time-varying environment (Gamelon *et al.* 2015).

The strong life-history patterns in our transient LTRE results additionally suggest that current conservation paradigms based on demographic patterns across life histories and the demographic buffering hypothesis of life-history evolution need to be revisited because of reliance on asymptotic analyses and stability of population structure. Our results offer initial

insight into the ways in which vital rates and components of population structure might contribute to temporal variation in realised population growth rates across species. Yet, our ideas need to be tested with empirical data and with models allowing for greater life cycle structure than our simple two-stage model. Where empirical data are (or become) available, our new transient LTREs could readily be used to reasses the demographic drivers of population dynamics across species and life-history strategies.

As ecologists strive to become better at forecasting (Petchey *et al.* 2015), it will be necessary to understand the mechanisms responsible for change in population dynamics and mean fitness in the non-stationary environments that are so prevalent during the Anthropocene (Wolkovich *et al.* 2014). Using transient LTREs for Δlog λ_g, we found that, similar to the results for stationary variation in vital rates over time (Fig. 2), there are life-history patterns in the demographic drivers of Δlog λ_g between a stationary and subsequent non-stationary environment (Fig. 4). But, the life-history patterns can be weak relative to the effects induced by the particular vital rate that changes in a non-stationary manner (Fig. S5), indicating that (1) it will often be inappropriate to use stationary methods for addressing the impact of climate change on population performance (Gaillard *et al.* 2013), an inherently non-stationary issue, and (2) that given spatial heterogeneity in the way in which land-use, water-use

and climate change affect the demography of species with different life histories, it will be challenging to make generalisable predictions about the future fates of species. It might thus be time to shift current enamor with climate envelope predictions based on biogeographic patterns to more mechanistic studies of demography over space and time (e.g. Merow *et al.* 2014).

Future research should improve upon our transient LTRE for $\Delta \log \lambda_g$ by extending it to higher statistical moments, highlight the influence of correlation among vital rates (Davison *et al.* 2013), and develop second derivatives of the stochastic growth rate (and short-term analogue) with respect to change in underlying vital rates and population structure. Because time series of vital rates and population structure are needed to implement the transient LTREs, one might think that our new methods can only be applied to the limited situations where complete censuses can be achieved (e.g. Coulson *et al.* 2005). Bayesian integrated population models can nevertheless be used to relax this constraint by statistically leveraging information across available demographic data and simultaneously estimate vital rates, population structure, total abundance and realised population growth rates, even when some data are missing or indirectly related to latent parameters of interest (Kéry & Schaub 2012). Estimates of statistical uncertainty in demographic outcomes provided by such models (Schaub & Abadi 2011) can additionally be used to decide when second-order extensions of the transient LTREs should be pursued.

By acknowledging the manner in which population dynamics actually operate in time-variant environments (eqn 1), our transient LTREs coupled with integrated population models will allow for more accurate insight into the relative contributions of intrinsic (e.g. density dependence, a special type of non-stationarity) and extrinsic (e.g. climate) mechanisms that affect population growth and mean fitness, as channelled through vital rates and population structure. These new tools will in turn help researchers improve the explanatory power of models used to forecast future dynamics amidst global change (Gotelli & Ellison 2006).

AUTHOR CONTRIBUTIONS

DNK conceived the ideas, led the analysis and wrote the manuscript. DTI assisted with the simulations, contributed to the development of the ideas, and edited the manuscript. MS contributed to the ideas, provided assistance with the analysis and edited the manuscript. HC contributed to the development of the ideas, provided assistance with the analysis and helped considerably with editing the manuscript.

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