When is population structure important? Integrating transient dynamics and life-history theory

Running title: Transient dynamics and life-history theory.

James Cant[1,2*], Christina M. Hernández[1,3], David N. Koons[4], Dave J. Hodgson[5], Man Qi[1], Andrew Hector[1], Iain Stott[6,7], Roberto Salguero-Gómez[1*]

1. Department of Biology, University of Oxford, Oxford, UK.
2. Centro de Ciências do Mar e do Ambiente (MARE), Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal.
3. Department of Biological Sciences, Old Dominion University, Norfolk, Virginia, USA.
4. Department of Fish, Wildlife, and Conservation Biology, Colorado State University, USA.
5. Department of Ecology & Evolution, University of Exeter, UK.
6. School of Natural Sciences, University of Lincoln, Lincoln, UK.
7. Department of Biology, University of Southern Denmark, Denmark.

*Corresponding Authors: James Cant, jicant@ciencias.ulisboa.pt;
Rob Salguero-Gómez, rob.salguero@biology.ox.ac.uk

Authorship Statement: JC & RS-G developed the synthesis idea with further input from CH, DK & ST. JC & CH identified and extracted population models for analysis from a database curated by RS-G, while RS-G, DH & JC contributed population vectors. JC implemented all analyses, shaped by discussions between JC, CH, MQ & RS-G. RS-G led efforts to secure research funding, with IS and AH contributing as CoIs. JC led manuscript write-up with support from RS-G, with all coauthors contributing equally to the development of subsequent drafts.

Data Availability Statement: All demographic data used in this study are available from the open-source COMPADRE and COMADRE databases (https://compadre-db.org/), whilst the phylogenetic details used to compute the evolutionary distances between the species represented in our data sample were sourced from the Open Tree of Life (https://tree.opentreeoflife.org). The phylogenetic subtrees and annotated R scripts used for data extraction and analyses are publicly available on Zenodo (https://doi.org/10.5281/zenodo.22084137).

Competing Interest Statement: All authors declare no competing interests.

Keywords: Plants, Structured Population Models, Transient dynamics, Transient Life Table Response Experiment.

Abstract

Population dynamics are governed not just by the vital rates of the members of a population, but also by population structure (*i.e.*, the distribution of individuals along species life cycles). A conventional focus of population biology and viability analyses has been to determine the influence of vital rates on long-term predictions such as stable population growth rates. With increasing appreciation of the importance of transient dynamics caused by non-stable population structures, we challenge this conventional focus and encourage the integration of population structure in assessments of population performance and resilience. To underscore the importance of population structure to realised population performance, we apply a transient Life Table Response Experiment framework to 268 comparisons of observed variation in population performance across 56 plant species over differing time periods, locations, and/or experimental treatments. We emphasise how changes in population structure are as consequential in determining realised demographic performance as shifts in survival and fecundity, particularly in populations characterised by 'faster' life-histories and a more limited capacity for contributing offspring throughout their lifespan. Overall, quantifying how population structure affects realised population dynamics can reveal key mechanistic insights for enhancing our management of natural systems and our understanding of life-history variation.

1. Introduction

Prevailing understanding of life-history theory has been transformed over time to reflect our growing appreciation for the complex drivers of life-history variation (Murray *et al.* 2025; Nylin & Gotthard 1998; Stearns 1980, 2000; Stott *et al.* 2024). Life-history theory stems from selection theory predicated on resource availability (MacArthur 1962), with species classified based on their differential investments across reproductive output and somatic maintenance (*i.e.* survival and growth) to maintain *asymptotic* (*i.e.*, long-term) population performance (Caswell 1982; Salguero-Gómez & Gamelon 2021; Stearns 1976, 1989, 1992). Indeed, perturbation analyses, which can describe the sensitivity of any emergent population attribute to underlying changes in the individual-level vital rates of survival, growth, and reproduction (Caswell 2001, 2019; de Kroon *et al.* 1986), are typically focused on asymptotic population growth patterns (Crone *et al.* 2011). Life-history theory has since expanded to accommodate the fast-slow and reproductive parity continua (Bakewell *et al.* 2020; Blackburn 1991; Gaillard *et al.* 1989; Healy *et al.* 2019; Oli 2004; Salguero-Gómez *et al.* 2016). Along the fast-slow continuum, organisms are still positioned based on their relative longevity *vs.* growth and maturation rates (Stearns 1992), but variation in reproductive characteristics is now described separately along the reproductive parity continuum (Gaillard *et al.* 1989; Salguero-Gómez *et al.* 2016). Together, these axes better represent organisms, such as corals and trees, who despite their slow growth and longer lifespans, still exhibit high and frequent reproductive outputs. However, with additional axes proposed for explaining further aspects of life-history variation, such as dissociating offspring size from reproductive frequency (Bielby *et al.* 2007) and differing species responses to environmental stochasticity (Santos *et al.* 2024) and disturbance (Murray *et al.* 2025), we are still to fully comprehend the multidimensional space characterising life-history variation (Stott *et al.* 2024).

Whilst life-history theory was traditionally built on assumptions of asymptotic dynamics (Caswell 1982; Partridge & Harvey 1988), variation in realised (*i.e.*, observed) population growth trajectories often do not correlate with changes in the vital rates thought to most affect population performance (Coulson et al. 2005). Instead, realised population growth trajectories are more routinely dominated by *transient* population dynamics emerging from the interaction between continually changing vital rates and population structure (Hodgson *et al.* 2015; Koons *et al.* 2005, 2016; McDonald *et al.* 2016). To attain their asymptotic growth trajectories, populations require stationary environments (Caswell 2001; Tuljapurkar 1989, 1982; Tuljapurkar & Orzack 1980). As such, asymptotic demographic behaviours are rarely, if ever, observed in real-world settings (Morozov *et al.* 2020). Instead, recurrent disturbances such as fires, disease outbreaks, seasonal climates, and density-dependent mechanisms, coupled with direct anthropogenic impacts, maintain the realised dynamics of natural populations in a transient state (Hastings 2004; Koons *et al.* 2005). Thus, accounting for population structure, an approach rarely taken in demography (Crone *et al.* 2011; Maldonado-Chaparro *et al.* 2018), is required for obtaining a greater mechanistic understanding of population performance. Strong links between population life histories and transient population dynamics have been widely demonstrated (Capdevila et al. 2022; Gamelon et al. 2014; Iles et al. 2016; Sæther et al. 2013; White et al. 2022). However, establishing how life-history variation shapes realised population performance requires disentangling how vital rates and population structure contribute to population performance across taxa.

Here, we aim to challenge the traditional focus of life-history theory on longer-term population performance and to advance the integration of transient demographic theory and life-history evolution. We start by discussing transient demographic concepts and emphasise how transient dynamics are a foundational component of realised population dynamics. Next, we

introduce advances in the tools used to partition transient demographic drivers, allowing for partitioning and quantifying the relative impacts of vital rates and population structure on realised population performance. Applying a transient Life Table Response Experiment framework (Koons *et al.* 2016, 2017) across 268 comparisons of plant population dynamics (representing 56 species) over differing time periods, locations, and/or experimental treatments, we then show when population structure can become as consequential as vital rates in shaping the realised performance and life-histories of natural populations. Finally, we conclude by discussing the practical implications and challenges associated with incorporating population structure and transient dynamics into conservation and monitoring frameworks.

2. Transient dynamics: the natural state of natural systems

Demographic theory posits that, when at a stationary equilibrium, a population will change in size at a constant rate over time, termed its long-term population growth rate, λ (Groenendael *et al.* 1988; Lotka 1925). Underlying this constant rate of growth, the population's structure is also expected to remain consistent through time, termed its stable-state distribution (SSD, hereafter) (Caswell 2001; Fisher 1930). Away from equilibrium, however, changes to the underlying vital rates of a population elicit changes to the age- (Hoy *et al.* 2020), size- (Sommer *et al.* 2024), developmental stage- (Radchuk *et al.* 2013), or other state-distributions (*e.g.*, sex ratio (Coulson *et al.* 2001)) of its constituent individuals, which prevents attainment of its SSD and subsequently influences future vital rate patterns. Accordingly, realised population trajectories comprise the direct and indirect effects of stochastic and disturbance-induced variability across both individual-level vital rates and the structure of populations through time (Jenouvrier 2013; Koons *et al.* 2017) (Fig. 1A). These transient dynamics can manifest as either abrupt transitions or long, persistent

changes that appear stable when observed over shorter time scales (Hastings *et al.* 2018). Concurrently, transient dynamics can mask ecosystem collapse (Hock *et al.* 2024) whilst also underpinning the resilience of natural systems to recurrent disturbances (Capdevila *et al.* 2020). Consequently, identifying the drivers of transient dynamics is key to forecasting the responses of natural systems to ongoing global change (Hastings *et al.* 2018).

Reflecting the ubiquity of transient dynamics in nature, approaches have been developed to quantify the extent to which the realised transient dynamics of natural populations differ from their asymptotic expectations (Fig. 1B) (Koons *et al.* 2005; Stott *et al.* 2011). In their transient state, populations will change in size at a rate either faster or slower than their asymptotic growth rate (λ), referred to as amplification and attenuation, respectively (Townley *et al.* 2007; Townley & Hodgson 2008). Measures such as *reactivity* (Neubert & Caswell 1997) and *maximal amplification* (Stott et al. 2011) describe the first-time step and maximum increase in a population's amplified growth rate relative to λ, with *first-step attenuation* and *maximal attenuation* representing analogous measures of decreased population growth. Meanwhile, *population inertia* provides insight into how the subsequent realised density of a population differs from that expected under stationary conditions (Koons et al. 2007). Crucially, many of these existing measures of transient population dynamics can be computed as (1) transient bounds, representing the extreme potential of a population given observed changes to its underlying vital rates, (2) case-specific estimates explicitly accounting for the role of observed population structures in mediating transient behaviours, or as (3) probability density functions informing on the most likely responses of populations across all potential changes (Stott *et al.* 2011; Townley & Hodgson 2008). Subsequently, these measures have expanded both the empirical and

comparative assessment of transient dynamics across natural populations (*e.g*, (Gerber & Kendall 2016; Iles *et al.* 2016; Jelbert *et al.* 2019; McDonald *et al.* 2016; Shriver *et al.* 2019).

Ecological trajectories are rarely determined by asymptotic dynamics, with transient dynamics governing the dynamics and disturbance responses of natural populations (Hastings *et al.* 2018; Hodgson *et al.* 2015; Morozov *et al.* 2020). With transient amplification and attenuation reflecting the ability for populations to benefit from and/or withstand shifts in their underlying vital rates, transient population dynamics underpin plant species viability within variable environments (Ellis & Crone 2013; McDonald *et al.* 2016; Stott *et al.* 2010). Likewise, the prevalence of amplificatory behaviours within the dynamics of coral populations mediates their ability to establish within more seasonally variable high-latitude environments (Cant *et al.* 2022, 2023). Transient amplification is also a major determinant of invasive potential (Jelbert *et al.* 2019), while the transient dynamics arising from changes in seasonal fawn survival determine the viability of Sitka deer (*Odocoileus hemionus sitkensis*) populations (Gilbert *et al.* 2020). Such is the influence of transient dynamics in shaping the disturbance responses of natural populations that transient metrics now constitute a frequently used framework for quantifying demographic resilience (Capdevila *et al.* 2020; Hodgson *et al.* 2015).

Generally speaking, resilience comprises the ability for systems to resist disturbance and recover subsequently (Holling 1973; Isbell *et al.* 2026) without losing key functionality (Gunderson *et al.* 2012; Oliver *et al.* 2015). As such, by describing how the dynamics of populations are expected to change following some perturbation to their underlying vital rates and/or structure (*e.g*., amplification and attenuation), and the longevity of any arising transient behaviours (*e.g.*, convergence Caswell [2001]), measures of transient dynamics represent a comparative framework for quantifying aspects of demographic resilience (Capdevila *et al.* 2020).

Adopting this demographic resilience framework has provided extensive insights into the resilience of natural systems. Examples include revealing the differential recovery rates in primary *vs.* secondary forest communities following deforestation (Serra *et al.* 2021), the relationship between life-history strategies and disturbance responses (Capdevila *et al.* 2022; White *et al.* 2022), and how population-level responses to disturbances underpin the vulnerability of whole ecological communities (Field *et al.* 2019; Paniw *et al.* 2021). This resilience framework is also the basis of theoretical advancements evaluating how different disturbance regimes will reshape our understanding of population resilience (Cant *et al.* 2025; Tuljapurkar *et al.* 2023), and assessments of how density-dependent feedback modulates disturbance responses (Hernández *et al.* 2025). Overall, the demographic resilience framework holds potential for distilling how transient population dynamics have informed evolutionary responses to changes in environmental variability and the frequency of recurrent disturbances (Murray *et al.* 2025).

3. Life Table Response Experiments

To understand how transient population dynamics influence life-history variation and *vice versa*, we need tools for explicitly quantifying how both vital rates and population structure contribute to realised population performance. In this context, Life Table Response Experiments (LTREs) are a widely adopted approach for partitioning variation in some measure of population performance into the contributions of underlying demographic parameters (Caswell 1989, 1996a). Consider a series of treatments, either natural or experimentally imposed, from which arise a series of artificially or naturally varying environmental contexts. Across these differing environmental contexts, using perturbation analyses, one can predict how a population's performance would be expected to change following corresponding changes in the population's underlying vital rates

(Caswell 2001; de Kroon *et al.* 1986). However, if a particular vital rate is expected to exert a strong effect on population performance but does not vary across differing environmental contexts, then said vital rate cannot have affected observed changes in population performance. Instead, LTREs translate the observed individual-level effects of differing environments into the observed population-level effects of those environments (Caswell 2000). Formally introduced as part of studies into the effects of social variables on human population growth and the abiotic preferences of grain beetles (Birch 1953; Lotka 1936), LTREs initially gained popularity in environmental toxicology. Routinely, these toxicology assessments entailed evaluating how the individual-level survival, growth, and reproductive consequences of chronic exposure to pesticides, fertilisers, radiation, and metal contaminants impact intrinsic rates of population growth (r) in planktonic crustacean species (Allan & Daniels 1982; Daniels & Allan 1981; Fitzmayer *et al.* 1982; Gentile *et al.* 1982; Hummon & Hummon 1975; Marshall 1962; Rao & Sarma 1986; Walton *et al.* 1982; Winner & Farrel 1976). Meanwhile, Levin *et al.* (1996) present a comprehensive assay into how the contamination of estuarine waters with sewage, petrol, and blue-green algae effects long-term population growth rates (λ) in polychaete worms. LTREs have since become an established approach across both experimental and observational ecological research (Caswell 1996b, 2019); although more frequently as a feature of exploratory assessments rather than applied management (Crone *et al.* 2011).

In contemporary population ecology, the LTRE framework has been extensively used to partition the effects of shifts in individual-level survival, growth, and/or reproductive patterns on observed variation in asymptotic population growth rates (λ) (Crone *et al.* 2011). Briefly, this classical LTRE framework entails an iterative approach whereby the contribution of each underlying parameter (x) comprises the balance between the effect of changing x on λ when all

213 other parameters are held constant and the sensitivity of λ to changes in x. These contributions can
214 represent an observed effect on λ relative to a reference condition, such as an experimental control
215 (*fixed-design*), or an effect on the variance in λ across a sequence of scenarios (*random-design*).
216 This flexibility, coupled with a straightforward analytical pipeline, has afforded LTREs a
217 transformative role in our understanding of (1) ecological mechanisms such as density-dependence
218 (Fowler *et al.* 2006; Oli *et al.* 2001), coexistence (Fréville & Silvertown 2005; Griffith 2010;
219 Jongejans & De Kroon 2005; Williams & Crone 2006) and range expansions (Angert 2006;
220 Layton-Matthews *et al.* 2020; Moutouama *et al.* 2025), (2) organism responses to recurrent
221 disturbances (Carson *et al.* 2025; Elderd & Doak 2006; Kesler *et al.* 2008) and habitat
222 fragmentation (Martínez-Ramos *et al.* 2016), (3) sustainable harvest yields (Schmidt *et al.* 2011;
223 Zuidema *et al.* 2010), and (4) the drivers of viability in vulnerable species (Goldstein & Steiner
224 2020; Mercado-Molina *et al.* 2015; Soto-Santiago *et al.* 2017). Although commonplace, the
225 classical LTRE framework can also be applied to partition variance across other measures of
226 population performance aside from λ, such as dispersal ability (Caswell *et al.* 2003), net
227 reproductive rate (Levin *et al.* 1996), and sex ratio (Veran & Beissinger 2009).

228 Continued advances in LTRE approaches have since motivated the development of
229 stochastic and transient extensions to the framework (Caswell 2010; Davison *et al.* 2010; Koons
230 *et al.* 2016). Populations invariably exist in variable environments (Lande *et al.* 2003). Yet the
231 focus of classical LTREs on asymptotic, time-invariant measures of population performance
232 prevents accommodating temporal variation in how vital rates respond to natural environmental
233 stochasticity (Caswell 2010). Alternatively, measures of stochastic population growth rate (λ_S),
234 representing geometric-mean population growth rates observed across a series of successive time
235 intervals, better capture how temporal vital rate patterns influence longer-term population

performance (Lewontin & Cohen 1969). Stochastic LTREs (*s*LTRE, *sensu* (Caswell 2010; Davison *et al.* 2010)) allow for partitioning variance in λ_S across treatments (or environments) into the direct effects of the specific treatments and any within-treatment variance across individual vital rates. Indeed, by explicitly considering stochasticity within population dynamics, *s*LTREs have provided key insights into the maintenance of range distributions (Villellas *et al.* 2013), population responses to herbivory (Jacquemyn *et al.* 2012), the influence of sociality on population fitness (Busana *et al.* 2022), the evolution of life-histories in garter snakes (Miller *et al.* 2011), and the effects of climate-induced shifts in phenology (Iler *et al.* 2019). More recently, transient Life Table Response Experiments (*t*LTREs, *sensu* (Koons *et al.* 2016)) have also gained prominence for decomposing variance in population performance. Unlike previous retrospective population analyses, however, *t*LTREs explicitly resolve how the interactions between a population's underlying vital rates and structure inform its realised performance across differing environments (Box 1) (Koons *et al.* 2016, 2017). *t*LTREs have since provided detailed inference into the drivers of population performance across various mammal (*e.g.*, Christian *et al.* 2024; Dobson *et al.* 2024; Maldonado-Chaparro *et al.* 2018)) and bird species (*e.g.*, (Gibson *et al.* 2025; Layton-Matthews *et al.* 2021; Nater *et al.* 2023; Summers *et al.* 2024; Tenan *et al.* 2021).

Alongside advancements in LTRE approaches to accommodate stochastic and transient applications, recent progress has also been made in enhancing the accuracy of LTREs through the exactLTRE framework (Hernández et al. 2023). The conventional pipeline underlying LTRE applications relies on Taylor series approximation (Caswell 2001). Briefly, this approximation assumes that a mathematical relationship can be represented as an infinite sum of terms, allowing for the estimation of the relationship using its derivatives at a selected point. Consequently, conventional LTRE approaches can only provide a close but inexact quantification of the

contributions of underlying demographic parameters to observed variation in selected population performance attributes (Hernández *et al.* 2023). By adopting functional analysis of variance (fANOVA) (Ellner et al. 2019; Hooker 2007) in place of the Taylor series approximation, the exactLTRE framework overcomes this limitation (Hernández et al. 2023). Thus, implementing classical, stochastic, and transient LTREs using the exactLTRE pipeline allows for accurately partitioning observed variance in demographic performance across both the main effects of underlying parameters and their interactions. Together, these developments across LTRE approaches have cultivated a powerful toolbox ideal for understanding how life histories shape realised population performance.

4. Linking realised population structure and life-history variation

Despite strong links between variation in life-history strategies and transient population dynamics (*e.g.,* Capdevila *et al.* 2022; Gamelon *et al.* 2014; Iles *et al.* 2016; Sæther *et al.* 2013; White *et al.* 2022), how the effect of life-history variation on realised population performance is shaped by population structure remains untested (Koons *et al.* 2016). Concurrently, we present a comprehensive assessment of how population structure contributes to shaping realised population performance across life-history variation. We apply *t*LTREs across 268 comparisons of plant population dynamics (representing 56 species) over differing time periods, locations, and/or experimental treatments, sourced from the COMPADRE database (version 6.23.5.0) (Salguero-Gómez et al. 2015). Within our *t*LTRE framework, we adopt a modified version of the aforementioned exactLTRE methodology (Hernández *et al.* 2023), allowing us to take advantage of the fANOVA approach whilst partitioning observed variance in realised population growth rates into contributions from changes in population structure and individual-level vital rates. We

encourage readers less familiar with LTRE approaches, especially *t*LTREs, to refer to Box 1 for a full walkthrough of a *t*LTRE analysis prior to engaging our findings below. See also Appendix S1 for a detailed overview of our full methodology.

4.1. Mapping the contributions of population structure across life-history variation

Changes in population structure have consequences on realised plant population performance, an effect that appears somewhat shaped by phylogenetic ancestry (Fig. 2). Across 268 within-species comparisons of plant population dynamics over differing time periods, locations, and/or experimental treatments, we used *t*LTREs to partition variance in realised population growth rates, var($\lambda_{transient}$), into the contributions of changes in population structure ($\boldsymbol{n}$), survival (σ), development (γ), and fecundity (ϕ). Using Pagel's λ (Pagel 1999), we also calculated the strength of the phylogenetic signal across our contribution to var($\lambda_{transient}$) estimates. Briefly, we computed phylogenetic signal as a measure of how gradients in observed trait variance correlate with evolutionary variance-covariance captured by the branch distances across a population-level phylogenetic tree established for our population sample (see Appendix S1: *Establishing phylogenetic relationships*). Note the difference between λ (i.e., long-term population growth rate) and Pagel's λ, which is a measure of phylogenetic signal and varies between 0 (low) and 1 (high) reflecting the explanatory strength of species phylogenetic ancestry in shaping observed trait variance (Freckleton et al. 2002). We illustrate how changes in population structure, survival and fecundity contribute equally to increases in the variance observed in realised population growth rates across space and time (Fig. 2); with only the interactions between these changes capable of diminishing observed variance. Moreover, with strong evidence that these contributions are modulated by evolutionary mechanisms (*i.e.*, no overlap with zero in Pagel's λ 95% confidence

bounds), particularly the effects of survival and growth (Pagel's $\lambda > 0.9$), we show a similar significance of phylogenetic ancestry in determining the roles population structure and fecundity play in shaping realised population performance (Pagel's λ: n = 0.65 [95% CI: 0.37, 0.83]; ϕ = 0.77 [0.41, 0.90]; Fig. 2).

The contributions of population structure to variance in realised performance are greatest in populations with shorter generation times, shorter life expectancies, shorter reproductive windows, and earlier reproductive maturity (Fig. 3A). We used a phylogenetically-informed partial least squares analysis (pPLS) to assess how the contributions of survival, development, fecundity, and population structure to $var(\lambda_{transient})$ map across the population traits of generation time (*i.e.*, the mean time between the birth of a parent and its offspring, T), age at reproductive maturity (L_α), mean life expectancy (*i.e.*, average lifespan, η_e), and reproductive window (*i.e.*, the duration of reproduction, $L_{\alpha\text{-}\omega}$). Together, T, L_α, η_e, and $L_{\alpha\text{-}\omega}$ reflect a well-defined trait space for characterising species along the fast-slow and reproductive parity continua (Salguero-Gómez *et al.* 2016; Stott *et al.* 2024). Briefly, PLS is a multivariate approach for assessing the extent to which a series of independent variables can explain observed variance across some dependent variable(s). Using this approach allowed us to quantify how variance in the underlying sources of $var(\lambda_{transient})$ across populations correlates with variance in their life-history characteristics. Indeed, our findings here emphasise the central role that survival plays in influencing realised population performance in longer-lived species (Gaillard *et al.* 2005), as, across our population comparisons, contributions of survival (σ) to $var(\lambda_{transient})$ increase with increasing generation time (Fig. 3A). However, in populations with 'faster' life histories (*i.e.*, shorter generation times and life expectancies, and faster maturity) changes in population structure are a key determinant of realised plant population performance (Fig 3A). Relative life-history speed determines climate vulnerability (Compagnoni

et al. 2021), extinction risk (Mace *et al.* 2008; Staerk *et al.* 2019) and adaptability (Pearson *et al.* 2014), by illustrating how population structure mediates realised performance in shorter-lived species, our findings compound the need for considering population structure as part of ongoing conservation efforts (Gamelon *et al.* 2021).

While changes in fecundity contribute strongly to variation in the realised population performance of species considered more iteroparous (*i.e.*, with multiple reproductive cycles), the contributions of population structure to realised population performance are more important in semelparous (*i.e.*, with a single terminal reproductive episode and represented by perennial monocarpic species in our sample) than in iteroparous species (Fig. 3B). Using pPLS we assessed how the contributions of survival, development, fecundity, and population structure to var($\lambda_{transient}$) align along a continuum defined by Degree of Iteroparity (*S*, with higher/lower values reflecting greater iteroparity/semelparity respectively). The first component axis of this pPLS primarily describes a transitional shift in contributions to *var*($\lambda_{transient}$) from survival (r = -0.64) to fecundity (r = 0.91; Fig. 3B). It is this same axis that also best aligns with patterns in the contributions of changes in population structure and its interaction effects (r: $\boldsymbol{n}$ = -0.40; σ:γ:ϕ:$\boldsymbol{n}$ = -0.46). Likewise, this first component is the best descriptor of patterns in *S*, although the correlation is comparatively weak (r = 0.27). Subsequently, the role of population structure in determining realised population performance increases, alongside survival, in more semelparous species. Iteroparity affords species increased opportunity for contributing offspring throughout their life cycle, thus reducing the sensitivity of their populations to the loss of juvenile life stages (Jonsson & Ebenman 2001). Iteroparous species can also maximise their reproductive output during periods of favourable conditions (*e.g.*, masting), potentially buffering their demographic performance against increased stochasticity (Bogdziewicz *et al.* 2024). Alternatively, semelparous species are vulnerable to

stochastic shifts in survival that reduce the likelihood of individuals reaching reproductive maturity and their terminal reproductive event (Fisher & Salguero-Gomez 2026; Goldstein *et al.* 2017).

We emphasise the importance of population structure in contributing to variation in realised population performance, particularly in species with 'faster' life histories and limited potential for contributing offspring throughout their lifespan; a non-trivial sub-section of life-history variation. Previous work has similarly reported the importance of transient dynamics to the realised performance of plant populations positioned at the extremities of life-history complexity (*i.e.*, trees and semelparous shrubs) (McDonald *et al.* 2016; Stott *et al.* 2010). Contributions to variance in realised population performance comprise both the sensitivity of realised performance to underlying population parameters as well as the magnitude by which these parameters were observed to actually change (Koons *et al.* 2016). Many semelparous plant species benefit from fast population turnover and/or high reproductive output to quickly monopolise available resources (Bonser 2013; Gagnon & Platt 2008). Meanwhile, slow-growing tree species typically exist within dense forest ecosystems and need to take advantage of erratic canopy gap dynamics (Whitmore 1989). Accordingly, although manifesting through different mechanisms, these selective pressures similarly elevate the contribution of transient dynamics to realised population performance across differing life history strategies (Stott *et al.* 2010).

Longstanding perspectives in population ecology consider the structure of populations an outcome of their life-history-informed response to local environmental conditions (Albaladejo-Robles *et al.* 2023; Wright *et al.* 2019). Populations of species whose individuals display low survival rates, fast maturity, and high reproductive output are expected to have population structures biased towards smaller/younger/less-developed classes. Alternatively, populations of species with individuals displaying higher survival, slower growth, and low reproductive outputs

are more likely to be composed of larger/older/more-developed individuals. Yet, as we illustrate, population structure helps to shape realised population performance, sequentially underpinning population fitness under prevailing environmental conditions. Instead of being a consequence of life-history variation, population structure and how it interacts with individual-level survival, growth, and reproductive patterns to inform realised population performance is an integral component of life-history variation.

5. Informing conservation science with assessments of population structure

Variation across the dynamical responses of natural populations to localised environmental and anthropogenic pressures compounds the intricate and nuanced responses of biodiversity to ongoing global change (Oliver *et al.* 2016). Consequently, amidst calls for more proactive species-based conservation approaches (Cardillo *et al.* 2026), conservation decisions must be grounded in reliable forecasts of population trajectories (Cerini *et al.* 2023). With transient dynamics being a ubiquitous component of natural ecosystems (Hastings et al. 2018; Morozov et al. 2020), understanding and forecasting population trajectories requires recognising when changes in population structure are likely to play a dominant role in determining population performance (Koons et al. 2017). Here, through a retrospective analysis of 268 natural populations, we have illustrated how contributions from transient changes in population structure can be as consequential, if not more so, than the direct contributions of changes in individual-level vital rates to realised population performance. However, empirical records detailing changes in population structure remain routinely undervalued across ecological and conservation science (Gascoigne *et al.* 2023; Koons *et al.* 2016).

Demographic data are an invaluable conservation resource (Conde *et al.* 2019; Le Coeur *et al.* 2026) as they offer compelling insight into the drivers of population invasion (Jelbert *et al.* 2019), decline (Warlick *et al.* 2024), and recovery (Morrison *et al.* 2016). However, accurately forecasting population trajectories requires long-term data that allow for predicting realised species responses to localised stressors and conservation action rather than their expected asymptotic responses. While this statement encapsulates unresolved uncertainties and challenges across population ecology, it does emphasise the need for systematically monitoring population structure. Quantifying trends in population abundances is already a central component of conservation science and evaluating species extinction risk (De Lima *et al.* 2024; Dietzel *et al.* 2021). Indeed, the IUCN recommends the monitoring of population sizes as part of its prioritisation of species for conservation effort (Mace *et al.* 2008), and its evaluation of conservation success (Akçakaya *et al.* 2018). Yet, although wildlife monitoring programs incorporating records of population structure into viability assessments do exist (*e.g.*, NOAA's Pacific salmon [*Oncorhynchus spp.*] monitoring service (Buhle *et al.* 2018)), assessments of population structure within species conservation assessments are not commonplace. Accordingly, biodiversity management and conservation approaches are neglecting a key determinant of future population trajectories (Gamelon *et al.* 2021). Future monitoring efforts and management frameworks aimed at assessing and maintaining population viability must therefore place greater emphasis on collecting, estimating, and incorporating information on population structure. We also encourage authors to make such information publicly available to facilitate continued advancements in ecological theory linking population structure, population performance, and life-history variation.

Approaches already exist for estimating latent population structure and its impact on population viability from established monitoring data using data integration. Integrated population

models allow for synthesising population census and productivity datasets into a single analysis pipeline for simultaneously estimating vital rates and population size (Besbeas *et al.* 2002; Brooks *et al.* 2004). Briefly, integrated population models use time-series population count data and basic species life cycle details to infer the vital rates needed to realise observed population trajectories (Schaub & Abadi 2011). Thus, integrated population models can be used to appropriately model the implicit feedback between the structure and underlying vital rates of natural populations (Plard *et al.* 2019), informing their responses to extrinsic and intrinsic perturbations (Koons *et al.* 2016). By explicitly considering the link between population structure and realised population performance, integrated population models can also account for how density dependence, metapopulation dynamics, and individual heterogeneity shape population trajectories (Plard *et al.* 2019; Schaub *et al.* 2015; Zipkin & Saunders 2018). Moreover, data integration is an effective approach for quickly identifying data gaps and thus can be used to guide research prioritisation (Zipkin & Saunders 2018). Yet, despite these strengths, data integration approaches have largely been used to develop demographic theory rather than for applied conservation (Oppel *et al.* 2014).

Beyond existing modelling frameworks, biodiversity monitoring is being flooded with technological developments advancing our capacity for distilling the structures of natural populations (Sutherland *et al.* 2026). Contemporary remote image-based tracking technologies allow identification of individual animals and understanding their behaviours at unprecedented resolutions and scales (Dell *et al.* 2014). For instance, camera-mounted unmanned aerial vehicles can alleviate access barriers associated with capturing the size distributions of isolated marine mammal populations (Stone & Davis 2025). AI-assisted photo processing can also distinguish between individual insects during light trapping exercises (Roy *et al.* 2024), and extract encounter data whilst recognising repeat individuals from photos of African megafauna (Gholami *et al.* 2026;

Vukelić *et al.* 2026). There is even scope for future extensions to detect and identify individuals from footfall signals recorded on seismic sensors (Steinmann *et al.* 2025). Meanwhile, public access to unparalleled quantities of high-resolution satellite imagery can expedite the collection of demographic data and population size structures for a variety of plant species at the country and continental scales (Fenollosa *et al.* 2025). At more local scales, the segmentation of aerial hyperspectral LiDAR datasets and underwater photomosaics facilitates distinguishing between individual tree crowns and coral colonies across dense forest and reef ecosystems (Dash *et al.* 2019; Maschler *et al.* 2018; Pavoni *et al.* 2022). Accordingly, efforts to consolidate forecasts of realised population trajectories across applied conservation and management must capitalise on these emerging tools as practical solutions for quantifying the structures of natural populations at scale.

6. Conclusions

The *realised* performance of any natural population is determined by its transient dynamics (Hodgson *et al.* 2015; Koons *et al.* 2005). Yet, our understanding of life-history variation and how it shapes the responses of natural populations to global change is rooted in assumptions of asymptotic dynamics that are rarely attained in nature. Transient population dynamics emerge from the interaction between vital rates and population structure (Jenouvrier 2013; Maldonado-Chaparro *et al.* 2018). Thus, population structure is a major driver of realised population performance (Koons *et al.* 2017). The urgent need to better understand the link between life histories and realised population performance (Stott *et al.* 2024; Sutherland *et al.* 2013) has heralded demographic tools for partitioning the contributions of both vital rates and structure to realised population performance (Koons *et al.* 2016). However, we still lack understanding of how

population structure shapes realised population performance across life-history variation (Maldonado-Chaparro *et al.* 2018). Using 268 comparisons of population dynamics of 56 plant species across differing time periods, locations, and/or experimental treatments, we used a *t*LTRE framework to assess how population structure informs demographic performance across axes of life-history variation. We illustrate that population structure can contribute as much as vital rates to realised population performance, particularly in 'faster-lived' species. Subsequently, conservation and research efforts that ignore population structure will continue to overlook a major determinant of current and future population performance.

Acknowledgements

J.C. and C.H. were supported by a NERC Pushing the Frontiers grant (NE/X013766/1) to R.S.G., I.S. & A.H. C.H. was also partly supported by a Marie Curie Fellowship (MSCA DensPopDy #10115386) with funding through UKRI (EP/Z002826/1), hosted by R.S.G. M.Q. was supported by a Marie Curie Fellowship (MSCA TraitMatter #101146302) with funding through UKRI (EP/Z00232X/1), hosted by R.S.G. DJH was supported by the University of Exeter; DNK was supported by a Fulbright award to the University of Exeter. I.S. was partly supported by a Novo Nordisk Fonden RECRUIT sabbatical grant (NNF25OC0103114).

References

Akçakaya, H.R., Bennett, E.L., Brooks, T.M., Grace, M.K., Heath, A., Hedges, S., *et al.* (2018). Quantifying species recovery and conservation success to develop an IUCN Green List of Species. *Conserv. Biol.*, 32, 1128–1138.

Albaladejo-Robles, G., Böhm, M. & Newbold, T. (2023). Species life-history strategies affect population responses to temperature and land-cover changes. *Glob. Change Biol.*, 29, 97–109.

Allan, J.D. & Daniels, R.E. (1982). Life table evaluation of chronic exposure to Eurytemora affinis (Copepoda) to kepone. *Mar. Biol.*, 66, 179–184.

Angert, A.L. (2006). Demography of Central and Marginal Populations of Monkeyflowers (Mimulus cardinalis and M. Lewisii). *Ecology*, 87, 2014–2025.

Bakewell, A.T., Davis, K.E., Freckleton, R.P., Isaac, N.J.B. & Mayhew, P.J. (2020). Comparing Life Histories across Taxonomic Groups in Multiple Dimensions: How Mammal-Like Are Insects? *Am. Nat.*, 195, 70–81.

Besbeas, P., Freeman, S.N., Morgan, B.J.T. & Catchpole, E.A. (2002). Integrating Mark–Recapture–Recovery and Census Data to Estimate Animal Abundance and Demographic Parameters. *Biometrics*, 58, 540–547.

Bielby, J., Mace, G.M., Bininda-Emonds, O.R.P., Cardillo, M., Gittleman, J.L., Jones, K.E., *et al.* (2007). The Fast-Slow Continuum in Mammalian Life History: An Empirical Reevaluation. *Am. Nat.*, 169, 748–757.

Birch, L.C. (1953). Experimental background to the study of the distribution and abundance of insects: I. The Influence of Temperature, Moisture and Food on the Innate Capacity for Increase of Three Grain Beetles. *Ecology*, 34, 698–711.

Blackburn, T.M. (1991). Evidence for a `Fast--Slow' Continuum of Life-History Traits Among Parasitoid Hymenoptera. *Funct. Ecol.*, 5, 65–74.

Bogdziewicz, M., Kelly, D., Ascoli, D., Caignard, T., Chianucci, F., Crone, E.E., *et al.* (2024). Evolutionary ecology of masting: mechanisms, models, and climate change. *Trends Ecol. Evol.*, 39, 851–862.

Bonser, S.P. (2013). High reproductive efficiency as an adaptive strategy in competitive environments. *Funct. Ecol.*, 27, 876–885.

Brooks, S.P., King, R. & Morgan, B.J.T. (2004). A Bayesian approach to combining animal abundance and demographic data. *Anim. Biodivers. Conserv.*, 27, 515–529.

Buhle, E.R., Scheuerell, M.D., Cooney, T.D., Ford, M.J., Zabel, R.W. & Thorson, J.T. (2018). *Using integrated population models to evaluate fishery and environmental impacts on Pacific salmon viability*. NOAA Technical Memorandum NMFS-NWFSC-140. US Department of Commerce.

Busana, M., Childs, D.Z., Burke, T.A., Komdeur, J., Richardson, D.S. & Dugdale, H.L. (2022). Population level consequences of facultatively cooperative behaviour in a stochastic environment. *J. Anim. Ecol.*, 91, 224–240.

Cant, J., Cook, K., Reimer, J.D., Mezaki, T., Nakamura, M., O'Flaherty, C., *et al.* (2022). Transient amplification enhances the persistence of tropicalising coral populations in marginal high latitude environments. *Ecography*.

Cant, J., Hernández, C.M., Thornley, R.H., Hector, A., Stott, I., & Salguero-Gómez, Roberto. (2025). Current estimates of population resilience do not predict resilience to directional environmental shifts. *BioRxiv*.

Cant, J., Reimer, J.D., Sommer, B., Cook, K., Kim, S.W., Sims, C.A., *et al.* (2023). Coral assemblages at higher latitudes favour short-term potential over long-term performance. *Ecology*, 00.

Capdevila, P., Stott, I., Beger, M. & Salguero-Gómez, R. (2020). Towards a comparative framework of demographic resilience. *Trends Ecol. Evol.*, 35, 776–786.

Capdevila, P., Stott, I., Cant, J., Beger, M., Grace, M. & Salguero-Gómez, R. (2022). Life history mediates the trade-offs among different components of demographic resilience. *Ecol. Lett.*, 00, 1–14.

Cardillo, M., Scheele, B.C. & Tulloch, A.I.T. (2026). Forecasting extinction risk for future-proof conservation decisions. *Trends Ecol. Evol.*, 41, 112–119.

Carson, B.D., Orians, C.M. & Crone, E.E. (2025). Context-dependent effects of a cryptic virus on butterfly population dynamics. *Ecology*, 106, e70199.

Caswell, H. (1982). Life History Theory and the Equilibrium Status of Populations. *Am. Nat.*, 120, 317–339.

Caswell, H. (1989). Analysis of life table response experiments I. Decomposition of effects on population growth rate. *Ecol. Model.*, 46, 221–237.

Caswell, H. (1996a). Analysis of life table response experiments II. Alternative parameterizations for size- and stage-structured models. *Ecol. Model.*, 88, 73–82.

Caswell, H. (1996b). Demography Meets Ecotoxicology: Untangling the Population Level Effects of Toxic Substances. In: *Ecotoxicology: A Hierarchical Treatment*. CRC Press, Florida, pp. 255–292.

Caswell, H. (2000). Prospective and retrospective perturbation analyses: Their roles in conservation biology. *Ecology*, 81, 619–627.

Caswell, H. (2001). *Matrix population models: Construction, analysis and interpretation*. Oxford University Press Inc.

553 Caswell, H. (2010). Life table response experiment analysis of the stochastic growth rate. *J. Ecol.*,
554 98, 324–333.
555 Caswell, H. (2019). *Sensitivity Analysis: Matrix Methods in Demography and Ecology*. Springer,
556 Cham.
557 Caswell, H., Lensink, R. & Neubert, M.G. (2003). Demography and Dispersal: Life Table
558 Response Experiments for Invasion Speed. *Ecology*, 84, 1968–1978.
559 Cerini, F., Childs, D.Z. & Clements, C.F. (2023). A predictive timeline of wildlife population
560 collapse. *Nat. Ecol. Evol.*, 7, 320–331.
561 Christian, M., Oosthuizen, W.C., Bester, M.N. & de Bruyn, P.J.N. (2024). Robustly estimating the
562 demographic contribution of immigration: Simulation, sensitivity analysis and seals. *J.*
563 *Anim. Ecol.*, 93, 632–645.
564 Compagnoni, A., Levin, S., Childs, D.Z., Harpole, S., Paniw, M., Römer, G., *et al.* (2021).
565 Herbaceous perennial plants with short generation time have stronger responses to climate
566 anomalies than those with longer generation time. *Nat. Commun.*, 12, 1–8.
567 Conde, D.A., Staerk, J., Colchero, F., Da Silva, R., Schöley, J., Maria Baden, H., *et al.* (2019).
568 Data gaps and opportunities for comparative and conservation biology. *PNAS*, 116, 9658–
569 9664.
570 Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H.,
571 *et al.* (2001). Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep.
572 *Science*, 292, 1528–1531.
573 Coulson, T., Gaillard, J.-M. & Festa-Bianchet, M. (2005). Decomposing the Variation in
574 Population Growth into Contributions from Multiple Demographic Rates. *J. Anim. Ecol.*,
575 74, 789–801.

576 Crone, E.E., Menges, E.S., Ellis, M.M., Bell, T., Bierzychudek, P., Ehrlén, J., *et al.* (2011). How
577 do plant ecologists use matrix population models? *Ecol. Lett.*, 14, 1–8.
578 Daniels, R.E. & Allan, J.D. (1981). Life table evaluation of chronic exposure to a pesticide. *Can J*
579 *Fish Aquat Sci*, 38, 485–494.
580 Dash, J.P., Watt, M.S., Paul, T.S.H., Morgenroth, J. & Pearse, G.D. (2019). Early Detection of
581 Invasive Exotic Trees Using UAV and Manned Aircraft Multispectral and LiDAR Data.
582 *Remote Sens.*, 11, 1812.
583 Davison, R., Jacquemyn, H., Adriaens, D., Honnay, O., de Kroon, H. & Tuljapurkar, S. (2010).
584 Demographic effects of extreme weather events on a short-lived calcareous grassland
585 species: Stochastic life table response experiments. *J. Ecol.*, 98, 255–267.
586 De Lima, R.A.F., Dauby, G., De Gasper, A.L., Fernandez, E.P., Vibrans, A.C., Oliveira, A.A.D.,
587 *et al.* (2024). Comprehensive conservation assessments reveal high extinction risks across
588 Atlantic Forest trees. *Science*, 383, 219–225.
589 Dell, A.I., Bender, J.A., Branson, K., Couzin, I.D., Polavieja, G.G. de, Noldus, L.P.J.J., *et al.*
590 (2014). Automated image-based tracking and its application in ecology. *Trends Ecol. Evol.*,
591 29, 417–428.
592 Dietzel, A., Bode, M., Connolly, S.R. & Hughes, T.P. (2021). The population sizes and global
593 extinction risk of reef-building coral species at biogeographic scales. *Nat. Ecol. Evol.*, 5,
594 663–669.
595 Dobson, F.S., Koons, D.N., Saraux, C., Tamian, A., Oli, M.K. & Viblanc, V.A. (2024). The
596 Demographic Basis of Population Growth: A 32-Year Transient Life Table Response
597 Experiment. *Ecol. Lett.*, 27, e14512.

598 Elderd, B.D. & Doak, D.F. (2006). Comparing the Direct and Community-Mediated Effects of
599 Disturbance on Plant Population Dynamics: Flooding, Herbivory and Mimulus guttatus. *J.*
600 *Ecol.*, 94, 656–669.
601 Ellis, M.M. & Crone, E.E. (2013). The role of transient dynamics in stochastic population growth
602 for nine perennial plants. *Ecology*, 94, 1681–1686.
603 Ellner, S.P., Snyder, R.E., Adler, P.B. & Hooker, G. (2019). An expanded modern coexistence
604 theory for empirical applications. *Ecol. Lett.*, 22, 3–18.
605 Fenollosa, E., Cohen, G. & Salguero-Gómez, R. (2025). Retrospective image analysis for long-
606 term demography using Google Earth imagery.
607 Field, C.R., Ruskin, K.J., Cohen, J.B., Hodgman, T.P., Kovach, A.I., Olsen, B.J., *et al.* (2019).
608 Framework for quantifying population responses to disturbance reveals that coastal birds
609 are highly resilient to hurricanes. *Ecol. Lett.*, 22, 2039–2048.
610 Fisher, D.O. & Salguero-Gomez, R. (2026). Evidence for adaptive explanations of semelparity in
611 animals. *Biol. Rev.*, 1–19.
612 Fisher, R.A. (1930). *The Genetical Theory of Natural Selection*. Oxford University Press, London.
613 Fitzmayer, K.M., Geiger, J.G. & Van Den Avyle, M.J. (1982). Effects of chronic exposure to
614 simazine on the cladoceran, Daphnia pulex. *Arch Env. Contam Toxicol*, 11, 603–609.
615 Fowler, N.L., Overath, R.D. & Pease, C.M. (2006). Detection of density dependence requires
616 density manipulations and calculation of λ. *Ecology*, 87, 655–664.
617 Fréville, H. & Silvertown, J. (2005). Analysis of interspecific competition in perennial plants using
618 Life Table Response Experiments. *Plant Ecol.*, 176, 69–78.
619 Gagnon, P.R. & Platt, W.J. (2008). Multiple Disturbances Accelerate Clonal Growth in a
620 Potentially Monodominant Bamboo. *Ecology*, 89, 612–618.

621 Gaillard, J., Yoccoz, N.G., Lebreton, J., Bonenfant, C., Devillard, S., Loison, A., *et al.* (2005).
622 Generation Time: A reliable metric to measure life-history variation
623 among mammalian populations. *Am. Nat.*, 166, 119–123.
624 Gaillard, J.-M., Pontier, D., Allainé, D., Lebreton, J.D., Trouvilliez, J. & Clobert, J. (1989). An
625 Analysis of Demographic Tactics in Birds and Mammals. *Oikos*, 56, 59–76.
626 Gamelon, M., Gimenez, O., Baubet, E., Coulson, T., Tuljapurkar, S. & Gaillard, J.M. (2014).
627 Influence of life-history tactics on transient dynamics: A comparative analysis across
628 mammalian populations. *Am. Nat.*, 184, 673–683.
629 Gamelon, M., Nater, C.R., Baubet, É., Besnard, A., Touzot, L., Gaillard, J.-M., *et al.* (2021).
630 Efficient use of harvest data: a size-class-structured integrated population model for
631 exploited populations. *Ecography*, 44, 1296–1310.
632 Gascoigne, S.J.L., Rolph, S., Sankey, D., Nidadavolu, N., Stell Pičman, A.S., Hernández, C.M., *et*
633 *al.* (2023). A standard protocol to report discrete stage-structured demographic
634 information. *Methods Ecol. Evol.*, 14, 2065–2083.
635 Gentile, J.H., Gentile, S.M., Hairston Jr., N.G. & Sullivan, B.K. (1982). The use of life-tables for
636 evaluating the chronic toxicity of pollutants to Mysidopsis bahia. *Hydrobiologia*, 93, 179–
637 187.
638 Gerber, B.D. & Kendall, W.L. (2016). Considering transient population dynamics in the
639 conservation of slow life-history species: An application to the sandhill crane. *Biol.*
640 *Conserv.*, 200, 228–239.
641 Gholami, S., Lee, D.E., Robinson, C., Bond, M.L., Dodhia, R. & Lavista Ferres, J.M. (2026). An
642 accurate, efficient, and accessible AI-powered solution for wildlife re-identification in
643 conservation. *Sci. Rep.*

644 Gibson, D., Arnold, T.W., Buderman, F.E. & Koons, D.N. (2025). Explaining the divergence of
645 population trajectories for two interacting waterfowl species. *Ecol. Monogr.*, 95, e1642.
646 Gilbert, S.L., Hundertmark, K.J., Lindberg, M.S., Person, D.K. & Boyce, M.S. (2020). The
647 Importance of Environmental Variability and Transient Population Dynamics for a
648 Northern Ungulate. *Front. Ecol. Evol.*, 8.
649 Goldstein, E.A., Merrick, M.J. & Koprowski, J.L. (2017). Functional semelparity drives
650 population dynamics and endangers a peripheral population. *Biol. Conserv.*, 205, 52–59.
651 Goldstein, J. & Steiner, U.K. (2020). Ecological drivers of jellyfish blooms – The complex life
652 history of a 'well-known' medusa (Aurelia aurita). *J. Anim. Ecol.*, 89, 910–920.
653 Griffith, A.B. (2010). Positive effects of native shrubs on Bromus tectorum demography. *Ecology*,
654 91, 141–154.
655 Groenendael, J. van, Kroon, H. de & Caswell, H. (1988). Projection matrices in population
656 biology. *Trends Ecol. Evol.*, 3, 264–269.
657 Gunderson, L.H., Allen, C.R. & Holling, C.S. (2012). *Foundations of Ecological Resilience*. Island
658 Press.
659 Hastings, A. (2004). Transients: The key to long-term ecological understanding? *Trends Ecol.*
660 *Evol.*, 19, 39–45.
661 Hastings, A., Abbott, K.C., Cuddington, K., Francis, T., Gellner, G., Lai, Y.C., *et al.* (2018).
662 Transient phenomena in ecology. *Science*, 361, 1–9.
663 Healy, K., Ezard, T.H.G., Jones, O.R., Salguero-Gómez, R. & Buckley, Y.M. (2019). Animal life
664 history is shaped by the pace of life and the distribution of age-specific mortality and
665 reproduction. *Nat. Ecol. Evol.*, 3, 1217–1224.

Hernández, C.M., Ellner, S.P., Adler, P.B., Hooker, G. & Snyder, R.E. (2023). An exact version of Life Table Response Experiment analysis, and the R package exactLTRE. *Methods Ecol. Evol.*, 14, 939–951.

Hernández, C.M., Stott, I., Koons, D.N. & Salguero-Gómez, R. (2025). Density dependence impacts our understanding of population resilience. *Am. Nat.*

Hock, K., Hastings, A., Doropoulos, C., Babcock, R.C., Ortiz, J.C., Thompson, A., *et al.* (2024). Transient dynamics mask the resilience of coral reefs. *Theor. Ecol.*, 17, 1–12.

Hodgson, D., McDonald, J.L. & Hosken, D.J. (2015). What do you mean, "resilient"? *Trends Ecol. Evol.*, 30, 503–506.

Holling, C.S. (1973). Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.*, 4, 1–23.

Hooker, G. (2007). Generalized Functional ANOVA Diagnostics for High-Dimensional Functions of Dependent Variables. *J. Comput. Graph. Stat.*, 16, 709–732.

Hoy, S.R., MacNulty, D.R., Smith, D.W., Stahler, D.R., Lambin, X., Peterson, R.O., *et al.* (2020). Fluctuations in age structure and their variable influence on population growth. *Funct. Ecol.*, 34, 203–216.

Hummon, W.D. & Hummon, M.R. (1975). Use of life table data in tolerance experiments. *Cah Biol Mar*, 16, 743–749.

Iler, A.M., Compagnoni, A., Inouye, D.W., Williams, J.L., CaraDonna, P.J., Anderson, A., *et al.* (2019). Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb. *J. Ecol.*, 107, 1931–1943.

Iles, D.T., Salguero-Gómez, R., Adler, P.B. & Koons, D.N. (2016). Linking transient dynamics and life history to biological invasion success. *J. Ecol.*, 104, 399–408.

689 Isbell, F., Mori, A.S., Loreau, M., Reich, P.B., Tilman, D., Anderson, M.I., *et al.* (2026). Predicting
690 temporal stability and resilience from resistance and recovery. *Nature*, 655, 394–400.
691 Jacquemyn, H., Brys, R., Davison, R., Tuljapurkar, S. & Jongejans, E. (2012). Stochastic LTRE
692 analysis of the effects of herbivory on the population dynamics of a perennial grassland
693 herb. *Oikos*, 121, 211–218.
694 Jelbert, K., Buss, D., McDonald, J., Townley, S., Franco, M., Stott, I., *et al.* (2019). Demographic
695 amplification is a predictor of invasiveness among plants. *Nat. Commun.*, 10, 1–6.
696 Jenouvrier, S. (2013). Impacts of climate change on avian populations. *Glob. Change Biol.*, 19,
697 2036–2057.
698 Jongejans, E. & De Kroon, H. (2005). Space versus time variation in the population dynamics of
699 three co-occurring perennial herbs. *J. Ecol.*, 93, 681–692.
700 Jonsson, A. & Ebenman, B. (2001). Are Certain Life Histories Particularly Prone to Local
701 Extinction? *J. Theor. Biol.*, 209, 455–463.
702 Kesler, H.C., Trusty, J.L., Hermann, S.M. & Guyer, C. (2008). Demographic responses of
703 Pinguicula ionantha to prescribed fire: a regression-design LTRE approach. *Oecologia*,
704 156, 545–557.
705 Koons, D.N., Arnold, T.W. & Schaub, M. (2017). Understanding the demographic drivers of
706 realized population growth rates. *Ecol. Appl.*, 27, 2102–2115.
707 Koons, D.N., Grand, J.B., Zinner, B. & Rockwell, R.F. (2005). Transient population dynamics:
708 Relations to life history and initial population state. *Ecol. Model.*, 185, 283–297.
709 Koons, D.N., Holmes, R.R. & Grand, J.B. (2007). Population inertia and its sensitivity to changes
710 in vital rates and population structure. *Ecology*, 88, 2857–2867.

711 Koons, D.N., Iles, D.T., Schaub, M. & Caswell, H. (2016). A life-history perspective on the
712 demographic drivers of structured population dynamics in changing environments. *Ecol.*
713 *Lett.*, 19, 1023–1031.
714 de Kroon, H., Plaisier, A., van Groenendael, J., Caswell, H., Thomas, S.C., Wallach, R., *et al.*
715 (1986). Elasticity: the relative contribution of demographic parameters to population
716 growth rate. *Ecology*, 67, 1427–1431.
717 Lande, R., Engen, S. & Sther, B.E. (2003). *Stochastic population dynamics in ecology and*
718 *conservation*. Oxford University Press, Oxford.
719 Layton-Matthews, K., Grøtan, V., Hansen, B.B., Loonen, M.J.J.E., Fuglei, E. & Childs, D.Z.
720 (2021). Environmental change reduces body condition, but not population growth, in a
721 high-arctic herbivore. *Ecol. Lett.*, 24, 227–238.
722 Layton-Matthews, K., Hansen, B.B., Grøtan, V., Fuglei, E. & Loonen, M.J.J.E. (2020).
723 Contrasting consequences of climate change for migratory geese: Predation, density
724 dependence and carryover effects offset benefits of high-arctic warming. *Glob. Change*
725 *Biol.*, 26, 642–657.
726 Le Coeur, C., Perret, J., Besnard, A., Cubaynes, S., Monchy, C., Naciri, M., *et al.* (2026).
727 Contribution and applications of demographic concepts to conservation. *Biol. Conserv.*,
728 316, 111776.
729 Levin, L., Caswell, H., Bridges, T., DiBacco, C., Cabrera, D. & Plaia, G. (1996). Demographic
730 Responses of Estuarine Polychaetes to Pollutants: Life Table Response Experiments. *Ecol.*
731 *Appl.*, 6, 1295–1313.
732 Lewontin, R.C. & Cohen, D. (1969). On population growth in a randomly varying environment.
733 *PNAS*, 62, 1056–1060.

734 Lotka, A.J. (1925). *Elements of Physical Biology*. Williams and Wilkins Company, Baltimore.
735 Lotka, A.J. (1936). The geographic distribution of intrinsic rate of natural increase in the United
736 States, and an examination of the relation between several measures of net reproductivity.
737 *J Am Stat Assoc*, 31, 273–294.
738 MacArthur, R.H. (1962). Some generalized theorems of natural selection, 48, 1893–1987.
739 Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N.,
740 *et al.* (2008). Quantification of Extinction Risk: IUCN's System for Classifying Threatened
741 Species. *Conserv. Biol.*, 22, 1424–1442.
742 Maldonado-Chaparro, A.A., Blumstein, D.T., Armitage, K.B. & Childs, D.Z. (2018). Transient
743 LTRE analysis reveals the demographic and trait-mediated processes that buffer population
744 growth. *Ecol. Lett.*, 21, 1693–1703.
745 Marshall, J.S. (1962). The effects of continuous gamma radiation on the intrinsic rate of natural
746 increase in Daphnia pulex. *Ecology*, 43, 598–607.
747 Martínez-Ramos, M., Ortiz-Rodríguez, I.A., Piñero, D., Dirzo, R. & Sarukhán, J. (2016).
748 Anthropogenic disturbances jeopardize biodiversity conservation within tropical rainforest
749 reserves. *Proc. Natl. Acad. Sci.*, 113, 5323–5328.
750 Maschler, J., Atzberger, C. & Immitzer, M. (2018). Individual Tree Crown Segmentation and
751 Classification of 13 Tree Species Using Airborne Hyperspectral Data. *Remote Sens.*, 10,
752 1218.
753 McDonald, J.L., Stott, I., Townley, S. & Hodgson, D.J. (2016). Transients drive the demographic
754 dynamics of plant populations in variable environments. *J. Ecol.*, 104, 306–314.

Mercado-Molina, A.E., Ruiz-Díaz, C.P., Pérez, M.E., Rodríguez-Barreras, R. & Sabat, A.M. (2015). Demography of the threatened coral Acropora cervicornis: implications for its management and conservation. *Coral Reefs*.

Miller, D.A., Clark, W.R., Arnold, S.J. & Bronikowski, A.M. (2011). Stochastic population dynamics in populations of western terrestrial garter snakes with divergent life histories. *Ecology*, 92, 1658–1671.

Morozov, A., Abbott, K., Cuddington, K., Francis, T., Gellner, G., Hastings, A., *et al.* (2020). Long transients in ecology: Theory and applications. *Phys. Life Rev.*, 32, 1–40.

Morrison, C.A., Robinson, R.A., Butler, S.J., Clark, J.A. & Gill, J.A. (2016). Demographic drivers of decline and recovery in an Afro-Palaearctic migratory bird population. *Proc. R. Soc. B Biol. Sci.*, 283, 20161387.

Moutouama, J.K., Compagnoni, A. & Miller, T.E.X. (2025). Forecasting range shifts of dioecious plants under climate change. *Proc. Natl. Acad. Sci.*, 122, e2422162122.

Murray, K., Townley, S. & Hodgson, D. (2025). A Disturbing View of Life History Evolution. *Am. Nat.*, 000–000.

Nater, C.R., Burgess, M.D., Coffey, P., Harris, B., Lander, F., Price, D., *et al.* (2023). Spatial consistency in drivers of population dynamics of a declining migratory bird. *J. Anim. Ecol.*, 92, 97–111.

Neubert, M.G. & Caswell, H. (1997). Alternatives to Resilience for Measuring the Responses of Ecological Systems to Perturbations. *Ecology*, 78, 653–665.

Nylin, S. & Gotthard, K. (1998). Plasticity in Life-History Traits. *Annu. Rev. Entomol.*, 43, 63–83.

Oli, M.K. (2004). The fast-slow continuum and mammalian life-history patterns: An empirical evaluation. *Basic Appl. Ecol.*, 5, 449–463.

778 Oli, M.K., Slade, N.A. & Dobson, F.S. (2001). Effect of density reduction on unita ground
779 squirrels: Analysis of life table response experiments. *Ecology*, 82, 1921–1929.
780 Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., *et al.* (2015).
781 Biodiversity and Resilience of Ecosystem Functions. *Trends Ecol. Evol.*, 30, 673–684.
782 Oliver, T.H., Smithers, R.J., Beale, C.M. & Watts, K. (2016). Are existing biodiversity
783 conservation strategies appropriate in a changing climate? *Biol. Conserv.*, 193, 17–26.
784 Oppel, S., Hilton, G., Ratcliffe, N., Fenton, C., Daley, J., Gray, G., *et al.* (2014). Assessing
785 population viability while accounting for demographic and environmental uncertainty.
786 *Ecology*, 95, 1809–1818.
787 Paniw, M., de la Riva, E.G. & Lloret, F. (2021). Demographic traits improve predictions of
788 spatiotemporal changes in community resilience to drought. *J. Ecol.*, 00, 1–13.
789 Partridge, L. & Harvey, P.H. (1988). The Ecological Context of Life History Evolution. *Science*,
790 241, 1449–1455.
791 Pavoni, G., Corsini, M., Ponchio, F., Muntoni, A., Edwards, C., Pedersen, N., *et al.* (2022).
792 TagLab: AI-assisted annotation for the fast and accurate semantic segmentation of coral
793 reef orthoimages. *J. Field Robot.*, 39, 246–262.
794 Pearson, R.G., Stanton, J. C., Shoemaker, K. T., Aiello-Lammens, M. E., Ersts, P. J., Horning, N.,
795 *et al.* (2014). Life history and spatial traits predict extinction risk due to climate change.
796 *Nat. Clim. Change*, 4, 217–221.
797 Plard, F., Fay, R., Kéry, M., Cohas, A. & Schaub, M. (2019). Integrated population models:
798 powerful methods to embed individual processes in population dynamics models. *Ecology*,
799 100, e02715.

800 Radchuk, V., Turlure, C. & Schtickzelle, N. (2013). Each life stage matters: the importance of
801 assessing the response to climate change over the complete life cycle in butterflies. *J. Anim.*
802 *Ecol.*, 82, 275–285.
803 Rao, T.R. & Sarma, S.S.S. (1986). Demographic parameters of Brachionis patulus Muller
804 (Rotifera) exposed to sublethal DDT concentrations at low and high food levels.
805 *Hydrobiologia*, 139, 193–200.
806 Roy, D.B., Alison, J., August, T.A., Bélisle, M., Bjerge, K., Bowden, J.J., *et al.* (2024). Towards
807 a standardized framework for AI-assisted, image-based monitoring of nocturnal insects.
808 *Philos. Trans. R. Soc. B Biol. Sci.*, 379.
809 Sæther, B.-E., Coulson, T., Grøtan, V., Engen, S., Altwegg, R., Armitage, K.B., *et al.* (2013). How
810 Life History Influences Population Dynamics in Fluctuating Environments. *Am. Nat.*, 182,
811 743–759.
812 Salguero-Gómez, R. & Gamelon, M. (2021). *Demographic Methods across the Tree of Life*.
813 Oxford University Press.
814 Salguero-Gómez, R., Jones, O.R., Archer, C.R., Buckley, Y.M., Che-Castaldo, J., Caswell, H., *et*
815 *al.* (2015). The COMPADRE Plant Matrix Database: An open online repository for plant
816 demography. *J. Ecol.*, 103, 202–218.
817 Salguero-Gómez, R., Jones, O.R., Jongejans, E., Blomberg, S.P., Hodgson, D.J., Mbeau-Ache, C.,
818 *et al.* (2016). Fast–slow continuum and reproductive strategies structure plant life-history
819 variation worldwide. *Proc. Natl. Acad. Sci.*, 113, 220–235.
820 Santos, G.S., Yang, X., Gascoigne, S.J.L., Compagnoni, A., Dias, A.T.C., Tuljapurkar, S., *et al.*
821 (2024). Population responses to environmental stochasticity are primarily driven by
822 survival-reproduction trade-offs and mediated by aridity.

Schaub, M. & Abadi, F. (2011). Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J. Ornithol.*, 152, 227–237.

Schaub, M., von Hirschheydt, J. & Grüebler, M.U. (2015). Differential contribution of demographic rate synchrony to population synchrony in barn swallows. *J. Anim. Ecol.*, 84, 1530–1541.

Schmidt, I.B., Mandle, L., Ticktin, T. & Gaoue, O.G. (2011). What do matrix population models reveal about the sustainability of non-timber forest product harvest? *J. Appl. Ecol.*, 48, 815–826.

Serra, R.T., Santos, C.D., Rousseau, G.X., Triana, S.P., Muñoz Gutiérrez, J.A. & Burgos Guerrero, J.E. (2021). Fast recovery of soil macrofauna in regenerating forests of the Amazon. *J. Anim. Ecol.*, 90, 2094–2108.

Shriver, R.K., Andrews, C.M., Arkle, R.S., Barnard, D.M., Duniway, M.C., Germino, M.J., *et al.* (2019). Transient population dynamics impede restoration and may promote ecosystem transformation after disturbance. *Ecol. Lett.*, 22, 1357–1366.

Sommer, B., Hodge, J.M., Lachs, L., Cant, J., Pandolfi, J.M. & Beger, M. (2024). Decadal demographic shifts and size-dependent disturbance responses of corals in a subtropical warming hotspot. *Sci. Rep.*, 14.

Soto-Santiago, F.J., Mercado-Molina, A., Reyes-Maldonado, K., Velez, Y., Ruiz-Diaz, C.P. & Sabat, A. (2017). Comparative demography of two common scleractinian corals: Orbicella annularis and Porites astreoides. *PeerJ*, 18.

Staerk, J., Conde, D.A., Ronget, V., Lemaitre, J.-F., Gaillard, J.-M. & Colchero, F. (2019). Performance of generation time approximations for extinction risk assessments. *J. Appl. Ecol.*, 56, 1436–1446.

Stearns, S.C. (1976). Life-History Tactics: A Review of the Ideas. *Q. Rev. Biol.*, 51, 3–47.

Stearns, S.C. (1980). A New View of Life-History Evolution. *Oikos*, 35, 266–281.

Stearns, S.C. (1989). Trade-Offs in Life-History Evolution. *Funct. Ecol.*, 3, 259–268.

Stearns, S.C. (1992). *The Evolution of Life Histories*. Oxford University Press, London.

Stearns, S.C. (2000). Life history evolution: successes, limitations, and prospects. *Naturwissenschaften*, 87, 476–486.

Steinmann, R., Nissen-Meyer, T., Cotton, F., Tilmann, F. & Mortimer, B. (2025). Decoding the footsteps of the African savanna: Classifying wildlife using seismic signals and machine learning. *Methods Ecol. Evol.*, 16, 819–836.

Stone, T.C. & Davis, K.J. (2025). Using unmanned aerial vehicles to estimate body volume at scale for ecological monitoring. *Methods Ecol. Evol.*, 16, 317–331.

Stott, I., Franco, M., Carslake, D., Townley, S. & Hodgson, D. (2010). Boom or bust? A comparative analysis of transient population dynamics in plants. *J. Ecol.*, 98, 302–311.

Stott, I., Salguero-Gómez, R., Jones, O.R., Ezard, T.H.G., Gamelon, M., Lachish, S., *et al.* (2024). Life histories are not just fast or slow. *Trends Ecol. Evol.*, 39, 830–840.

Stott, I., Townley, S. & Hodgson, D. (2011). A framework for studying transient dynamics of population projection matrix models. *Ecol. Lett.*, 14, 959–970.

Summers, J., Cosgrove, E.J., Bowman, R., Fitzpatrick, J.W. & Chen, N. (2024). Density dependence maintains long-term stability despite increased isolation and inbreeding in the Florida Scrub-Jay. *Ecol. Lett.*, 27, e14483.

Sutherland, W.J., Burgess, N.D., Edwards, S.V., Jones, J.P.G., Soltis, P.S., Tilman, D., *et al.* (2026). Nine changes needed to deliver a radical transformation in biodiversity measurement. *Proc. Natl. Acad. Sci.*, 123, e2519345123.

869 Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D.,
870 *et al.* (2013). Identification of 100 fundamental ecological questions. *J. Ecol.*, 101, 58–67.
871 Tenan, S., Becker, D., Tolkmitt, D. & Schaub, M. (2021). Decomposing fecundity and evaluating
872 demographic influence of multiple broods in a migratory bird. *J. Anim. Ecol.*, 90, 1071–
873 1084.
874 Townley, S., Carslake, D., Kellie-Smith, O., McCarthy, D. & Hodgson, D. (2007). Predicting
875 transient amplification in perturbed ecological systems. *J. Appl. Ecol.*, 44, 1243–1251.
876 Townley, S. & Hodgson, D.J. (2008). Erratum et addendum: Transient amplification and
877 attenuation in stage-structured population dynamics. *J. Appl. Ecol.*, 45, 1836–1839.
878 Tuljapurkar, S. (1989). An uncertain life: Demography in random environments. *Theor. Popul.*
879 *Biol.*, 35, 227–294.
880 Tuljapurkar, S., Jaggi, H., Gascoigne, S.J.L., Zuo, W., Kajin, M. & Salguero-Gómez, R. (2023).
881 From disturbances to nonlinear fitness and back.
882 Tuljapurkar, S.D. (1982). Population dynamics in variable environments. III. Evolutionary
883 dynamics of *r*-selection. *Theor. Popul. Biol.*, 21, 141–165.
884 Tuljapurkar, S.D. & Orzack, S.H. (1980). Population dynamics in variable environments I. Long-
885 run growth rates and extinction. *Theor. Popul. Biol.*, 18, 314–342.
886 Veran, S. & Beissinger, S.R. (2009). Demographic origins of skewed operational and adult sex
887 ratios: perturbation analyses of two-sex models. *Ecol. Lett.*, 12, 129–143.
888 Villellas, J., Morris, W.F. & García, M.B. (2013). Variation in stochastic demography between
889 and within central and peripheral regions in a widespread short-lived herb. *Ecology*, 94,
890 1378–1388.

Vukelić, M., White, E.W., Fennessy, J., Zabeirou, A.R.M., Gašparová, K., Valle, S., *et al.* (2026). Monitoring African Megafauna in an Anthropogenic Landscape: A 15-Year Case Study of the Vulnerable West African Giraffe. *Anim. Conserv.*, 29, 235–248.

Walton, W.E., Compton, S.M., Allan, J.D. & Daniels, R.E. (1982). The effect of acid stress on survivorship and reproduction of Daphnia pulex (Crustacea: Cladocera). *Can J Zool*, 60, 573–579.

Warlick, A.J., Himes Boor, G.K., McGuire, T.L., Shelden, K.E. w., Jacobson, E.K., Boyd, C., *et al.* (2024). Identifying demographic and environmental drivers of population dynamics and viability in an endangered top predator using an integrated model. *Anim. Conserv.*, 27, 240–252.

White, J.W., Barceló, C., Hastings, A. & Botsford, L.W. (2022). Pulse disturbances in age-structured populations: Life history predicts initial impact and recovery time. *J. Anim. Ecol.*, 91, 2370–2383.

Whitmore, T.C. (1989). Canopy Gaps and the Two Major Groups of Forest Trees. *Ecology*, 70, 536–538.

Williams, J.L. & Crone, E.E. (2006). The Impact of Invasive Grasses on the Population Growth of Anemone Patens, a Long-Lived Native Forb. *Ecology*, 87, 3200–3208.

Winner, R.W. & Farrel, M.P. (1976). Acute and chronic toxicity of copper to four species of Daphnia. *J Fish Res Board Can*, 33, 1685–1691.

Wright, J., Bolstad, G.H., Araya-Ajoy, Y.G. & Dingemanse, N.J. (2019). Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. *Biol. Rev.*, 94, 230–247.

913 Zipkin, E.F. & Saunders, S.P. (2018). Synthesizing multiple data types for biological conservation
914 using integrated population models. *Biol. Conserv.*, 217, 240–250.
915 Zuidema, P.A., Jongejans, E., Chien, P.D., During, H.J. & Schieving, F. (2010). Integral projection
916 models for trees: A new parameterization method and a validation of model output. *J.*
917 *Ecol.*, 98, 345–355.
918 Zúñiga-Vega, J.J., Valverde, T., Rojas-González, R.I. & Lemos-Espinal, J.A. (2007). Analysis of
919 the Population Dynamics of an Endangered Lizard (Xenosaurus Grandis) through the Use
920 of Projection Matrices. *Copeia*, 2007, 324–335.

Figures & Tables

Figure 1

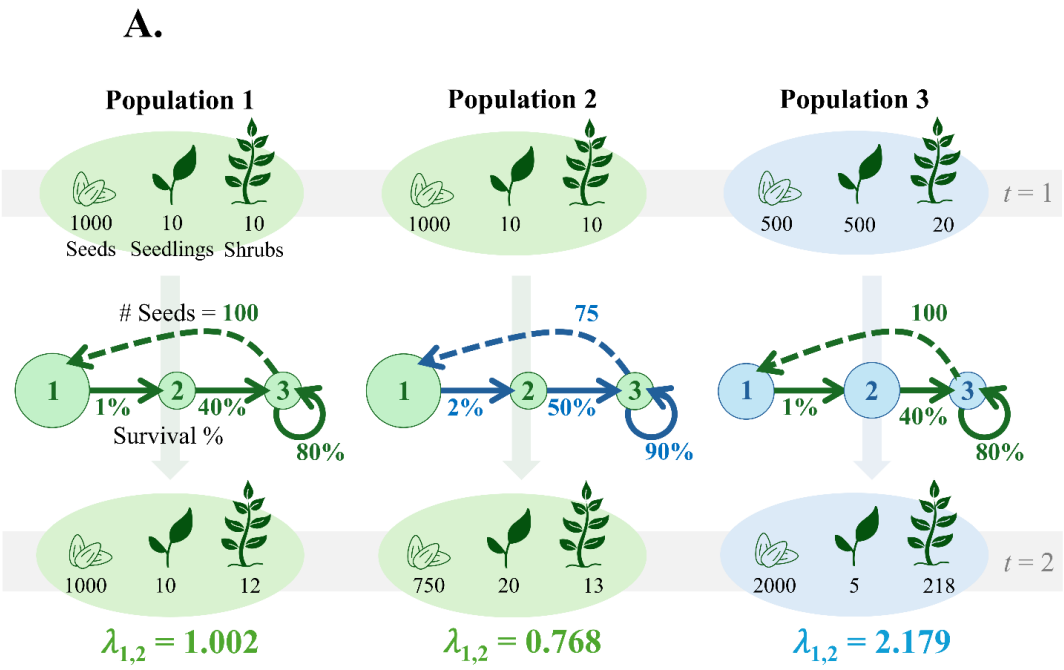

Figure 1. Realised population performance differs from stationary expectations and arises from the interaction between changes in individual-level vital rates and population structure. **(A)** Variation across the realised growth rates expressed by natural populations is underpinned by changes in both their underlying vital rates (*e.g.*, survival & fecundity) and structure (*i.e.*, the distribution of individuals across their life cycle). Consider three populations, each comprising the exact same population size (N_t = 1,020 individuals) at time t = 1. Two of these populations (Populations 1 & 2) have an identical structure but exhibit differing survival and fecundity rates, while two (Populations 1 & 3) have different structures but possess the same survival and fecundity rates. Despite these paired similarities, each population displays very different growth trajectories between times t = 1 and t = 2 owing to their differing structures and vital rates, with Population 1 remaining stable ($\lambda_{1,2} \approx 1$), Population 2 declining ($\lambda_{1,2} < 1$), and Population 3 growing rapidly ($\lambda_{1,2} >> 1$). **(B)** Various measures exist for quantifying the transient dynamics exhibited by natural populations existing away from their stationary equilibrium. These measures include *reactivity*, *maximal amplification*, and *upper inertia*, which describe the capacity for populations to undergo faster-than-expected growth (*i.e.*, amplification). Meanwhile, measures such as *first-step attenuation*, *maximal attenuation*, and *lower inertia* then describe the potential for populations to undergo slower-than-expected growth (*i.e.*, attenuation), while the *damping ratio* can be used to determine the expected time for any transient behaviours to converge back to a stationary equilibrium. Note that this is not an exhaustive list of available transient measures and is only intended to provide a flavour of the breadth of the transient demographic toolbox.

Figure 2

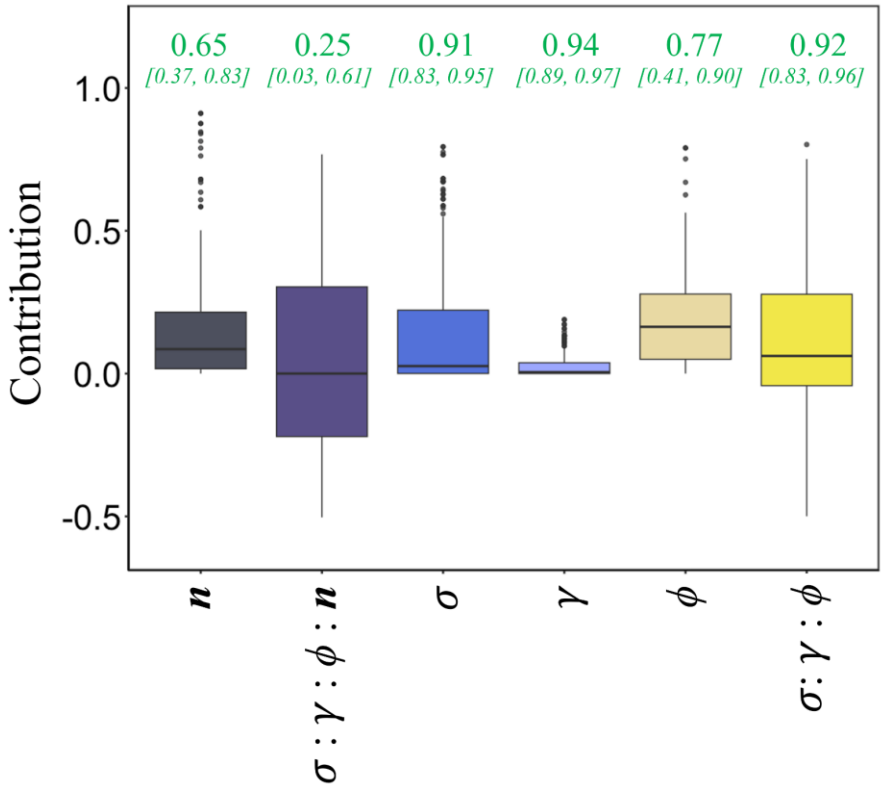

Figure 2. The effect of contributions from population structure on realised population performance is equivalent to those of survival and fecundity. The contributions of population structure (***n***), survival (σ), development (γ), fecundity (ϕ), and their interactions (σ:γ:ϕ:***n*** & σ:γ:ϕ) to observed variance in realised population growth rates ($\lambda_{transient}$). Inset values illustrate how gradients in observed trait variance correlate with evolutionary variance-covariance between populations captured by the branch distances across a phylogenetic tree created for our population sample. Error shown as 95% CIs.

952 **Figure 3**

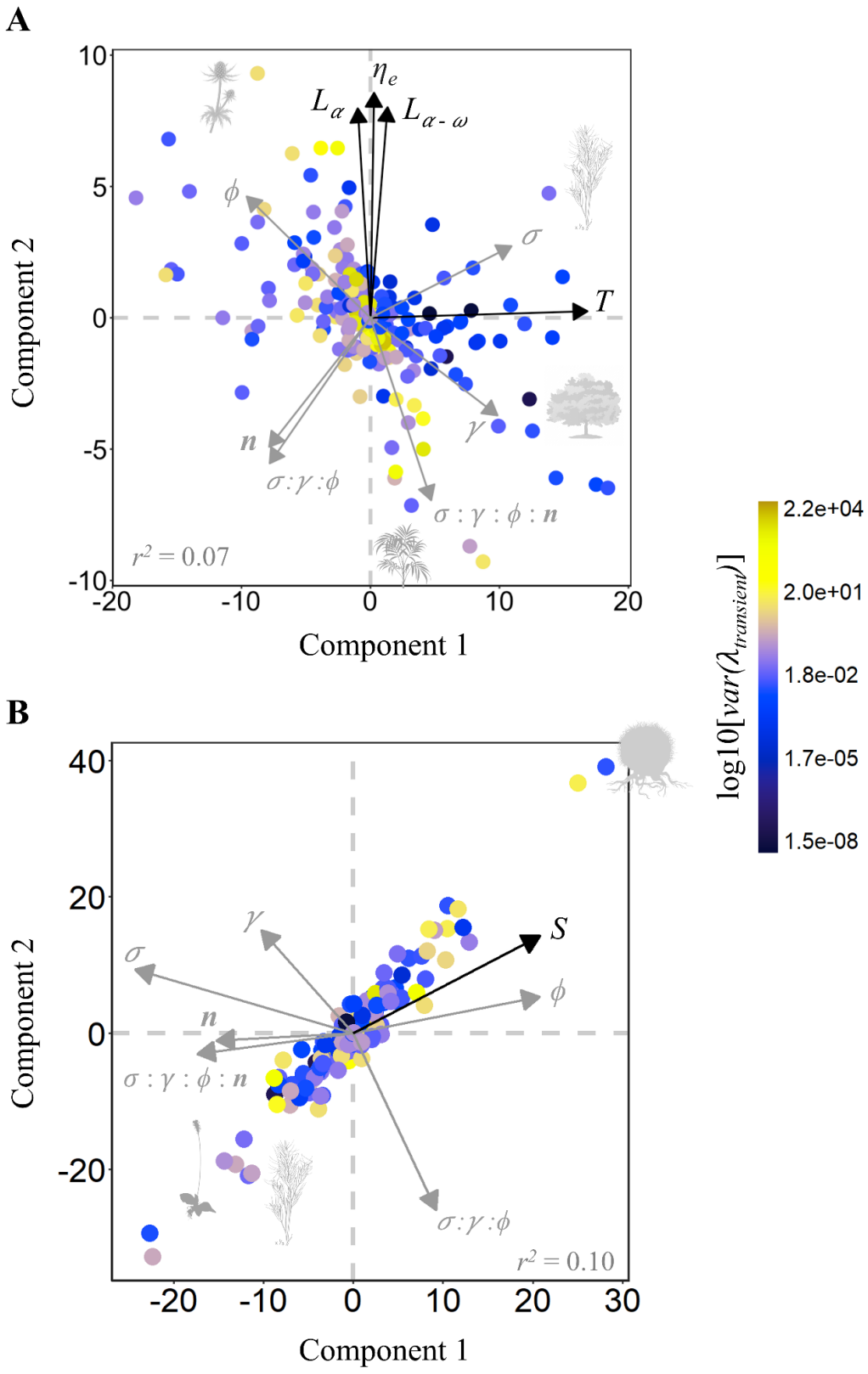
A
B
Component 1
Component 2
η_e
L_α
$L_{\alpha-\omega}$
ϕ
σ
T
γ
n
$\sigma:\gamma:\phi$
$\sigma:\gamma:\phi:n$
$r^2 = 0.07$
S
$r^2 = 0.10$
log10[$var(\lambda_{transient})$]
2.2e+04
2.0e+01
1.8e-02
1.7e-05
1.5e-08

Figure 3. Contributions from population structure to variation in realised population performance are greatest in species with faster life-histories and more limited opportunities for contributing offspring across their lifespan. Partial least squares biplots showing how variance in the contributions of population structure ($\boldsymbol{n}$), survival (σ), development (γ), fecundity (ϕ), and their interactions (σ:γ:ϕ:$\boldsymbol{n}$ & σ:γ:ϕ) to observed variation in $\lambda_{transient}$ across populations correlates with a populations' **(A)** position along the fast-slow continuum (defined by the traits of generation time [T], age at reproductive maturity [L_{α}], mean life expectancy [η_{e}], and reproductive window [$L_{\alpha\text{-}\omega}$]), and **(B)** degree of iteroparity (S). PLS biplots visualise the extent to which correlations between independent (black loading arrows) and dependent (grey loading arrows) variables explain observed variance across the selected dependent variables. Across both panels, point colour depicts associated log-transformed variance in $\lambda_{transient}$. Representative species icons included adjacent to corresponding data point showing (top to bottom): *Eryngium alpinum* (Alpine Sea holly), *Danthonia sericea* (Silky oat-grass), *Acer saccharum* (Sugar maple), *Chamaedorea elegans* (Parlour palm), *Mammillaria magnimamma* (Mexican pincushion), and *Plantago media* (Hoary plantain).

Box 1. tLTRE: an empirical example

We present a walkthrough of a *t*LTRE assessment of annual changes in the dynamics of a knob-scaled lizard population (*Xenosaurus grandis*) surveyed annually between 2000 and 2003 ($\boldsymbol{A}_x$) (Zúñiga-Vega *et al.* 2007) (Eq. 1). Briefly, these data describe changes in the probabilities of individuals transitioning between juvenile and adult stage classes (blue) and their per-capita fecundity (orange). Hypothetical counts of individuals per stage-class ($\boldsymbol{n}_x$) corresponding with these empirically observed vital rates have been added for the purposes of this example.

$$A_{2000/1} = \begin{bmatrix} 0.609 & 2.061 \\ 0.146 & 0.854 \end{bmatrix} \;\&\; n_{2000} = \begin{bmatrix} 50 \\ 50 \end{bmatrix} \qquad A_{2001/2} = \begin{bmatrix} 0.621 & 1.894 \\ 0.203 & 0.788 \end{bmatrix} \;\&\; n_{2001} = \begin{bmatrix} 154 \\ 50 \end{bmatrix}$$

$$A_{2002/3} = \begin{bmatrix} 0.550 & 1.385 \\ 0.231 & 0.576 \end{bmatrix} \;\&\; n_{2002} = \begin{bmatrix} 178 \\ 66 \end{bmatrix} \tag{1}$$

Asymptotic (λ) and realised population growth rates ($\lambda_{transient}$) across the three time-intervals illustrate differing growth trajectories. λ at time x is equal to the dominant eigenvalue of matrix $\boldsymbol{A}_x$, whereas $\lambda_{transient}$ is computed from associated matrices and population vectors (Eq. 2). Both measures reflect retrospective estimates of whether the population grew, remained constant, or declined (> 1, = 1, < 1, respectively) over the associated time interval.

$$\lambda_{transient} = \frac{\Sigma A_x n_x}{\Sigma n_x} \tag{2}$$

Asymptotic population growth estimates suggest that the population grew continually, but that growth slowed in the third year (λ = 1.29, 1.33 & 1.12), while $\lambda_{transient}$ estimates show that the population did indeed grow but at a much faster initial rate, and that growth slowed continuously across the three-year period ($\lambda_{transient}$: 1.84, 1.33 & 1.10). We can now estimate the variance in $\lambda_{transient}$ for the population ($var(\lambda_{transient})$ = 0.0938), and it is this value that forms the basis of our

*t*LTRE analysis. Note that $var(\lambda_{transient})$ here is equal to the mean of the squared deviation in $\lambda_{transient}$ estimates (Hernández *et al.* 2023).

Next, we partition variance in $\lambda_{transient}$ into the contributions of changes observed across the dynamics and structure of the population. First, we compute the mean dynamics ($\underline{\boldsymbol{A}}$) and population vector ($\underline{\boldsymbol{n}}$) (arithmetic element-by-element means, in each case) represented across the time series:

$$\bar{A} = \begin{bmatrix} 0.594 & 1.780 \\ 0.193 & 0.739 \end{bmatrix} \;\&\; \bar{n} = \begin{bmatrix} 120 \\ 55 \end{bmatrix} \tag{3}$$

Second, holding all other elements at their mean condition, we systematically replace the value of each matrix element and the population vector with their observed conditions across the time series. We then recalculate var($\lambda_{transient}$) using these modified $\boldsymbol{A}$ and $\boldsymbol{n}$ products. For instance, not only does the *X. grandis* population's structure change across the surveyed time intervals, but so does its per-capita fecundity. To quantify the first-order contribution of changes in per-capita fecundity on var($\lambda_{transient}$), we isolate the observed changes in fecundity whilst holding all other elements at their mean condition (Eq. 4).

$$A_{2000/1} = \begin{bmatrix} 0.594 & 2.061 \\ 0.193 & 0.739 \end{bmatrix} \;\&\; \bar{n} = \begin{bmatrix} 120 \\ 55 \end{bmatrix} \qquad A_{2001/2} = \begin{bmatrix} 0.594 & 1.894 \\ 0.193 & 0.739 \end{bmatrix} \;\&\; \bar{n} = \begin{bmatrix} 120 \\ 55 \end{bmatrix}$$

$$A_{2002/3} = \begin{bmatrix} 0.594 & 1.385 \\ 0.193 & 0.739 \end{bmatrix} \;\&\; \bar{n} = \begin{bmatrix} 120 \\ 55 \end{bmatrix} \tag{4}$$

The modified estimates of $\lambda_{transient}$ associated with this manipulation are 1.42, 1.37 & 1.21, such that changes in fecundity alone contribute to a $var(\lambda_{transient})$ of 0.0082 (8.8% of the true observed variance). Meanwhile, to quantify the contribution of population structure, we can isolate the effects of observed changes in structure alongside the population's mean dynamics (Eq. 5).

$$\bar{A} = \begin{bmatrix} 0.594 & 1.780 \\ 0.193 & 0.739 \end{bmatrix} \;\&\; n_{2000} = \begin{bmatrix} 50 \\ 50 \end{bmatrix} \qquad \bar{A} = \begin{bmatrix} 0.594 & 1.780 \\ 0.193 & 0.739 \end{bmatrix} \;\&\; n_{2001} = \begin{bmatrix} 134 \\ 50 \end{bmatrix}$$

$$\bar{A} = \begin{bmatrix} 0.594 & 1.780 \\ 0.193 & 0.739 \end{bmatrix} \;\&\; n_{2002} = \begin{bmatrix} 178 \\ 66 \end{bmatrix} \tag{5}$$

On this occasion, our modified estimates of $\lambda_{transient}$ are 1.65, 1.26 & 1.26, with population structure therefore contributing to a $var(\lambda_{transient})$ of 0.0346 (36.8% of the true observed variance). Repeating the above steps for all remaining elements illustrates how changes in population structure contribute more to $var(\lambda_{transient})$ than all vital rate transitions combined (0.0346 *vs.* 0.0107), with only the pooled interactions between the vital rates and population structure (0.0473) having a greater effect. However, these interaction effects are largely driven by contributions from the interaction between population structure and per-capita fecundity (0.0335). Overall, not only does this worked example demonstrate the power of *t*LTRE approaches for partitioning the drivers of realised population performance, but it also evidences the potential for population structure to impact population performance more than the vital rates.
