**Demographic buffering in natural populations: multi-level perspective**

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**Abstract** (147/150 words)

Environmental stochasticity impacts population dynamics and their viability. As such, understanding how organisms cope with this variability is crucial. Here, we investigate demographic buffering, the ability of populations to maintain stable growth despite environmental fluctuations. We integrate well-established stochastic and deterministic approaches to investigate characteristics of demographic buffering, analysing stochastic elasticities and self-second derivatives of deterministic population growth rate. We test the hypothesis that buffered species exhibit low stochastic elasticity to temporal variability and signs of concave selection (*i.e.* negative second derivatives of population growth rate with respect to demographic processes), reducing variance in key demographic processes. Analysing 43 natural populations of 37 mammal species, we find limited support for this hypothesis. Indeed, while primates often show low stochastic elasticity, concave selection is less prevalent than expected. Our findings highlight the complex and dynamic relationship between demographic processes, environmental variability, and selection pressures in determining population persistence.

**Introduction**

Environmental stochasticity shapes organisms’ life histories (Bonsall & Klug 2011; Stearns 1992; Tuljapurkar 1990, 2010). Nonetheless, how organisms will cope with the changing variation in environmental conditions (Bathiany *et al.* 2018; Boyce *et al.* 2006; Morris *et al.* 2008) remains an intriguing ecological and evolutionary question (Sutherland *et al.* 2013). Evolutionary demography offers a range of explanations for how evolutionary processes influence demographic responses to environmental variability (Charlesworth 1994; Healy *et al.* 2019; Hilde *et al.* 2020; Pfister 1998; Tuljapurkar *et al.* 2009). However, it is stochastic demography that explicitly addresses the impacts of fluctuating environments on wild populations of plants and animals (Boyce *et al.* 2006).

Stochastic demography is grounded in the powerful approximation introduced by Tuljapurkar (Tuljapurkar 1982). This approximation posits that the long-term stochastic population growth rate (*λs*) is directly related to the geometric mean of population growth rates over time (*λt*) and the variance-covariance structure of demographic processes (Boyce *et al.* 2006; Tuljapurkar 1982). An increase in the geometric mean of *λt* over time leads to a corresponding rise in *λs*. Conversely, higher variance in *λt* reduces *λs* (Morris & Doak 2004; Tuljapurkar 1982), thereby influencing population persistence (Lefèvre *et al.* 2016).

The ability of a population to diminish the effects of environmental stochasticity on *λs* — by keeping some demographic processes (as much as possible) constant over time — is called demographic buffering (Bjørkvoll *et al.* 2016; Gascoigne *et al.* 2023a, 2024b, a; Hilde *et al.* 2020; McDonald *et al.* 2016; Reed & Slade 2012; Rodríguez‐Caro *et al.* 2021). A way to test for demographic buffering is outlined by the demographic buffering hypothesis (Pfister 1998) (Box 1). The demographic buffering hypothesis extends Tuljapurkar’s approximation to state that negative covariance between *the impact of a demographic process on λt* (see Box 1 for details) and *how much a demographic process varies* through time would be optimal if such negative covariance could evolve (Le Coeur *et al.* 2022; Gaillard & Yoccoz 2003; Morris & Doak 2004; Pélabon *et al.* 2020; Pfister 1998). Evidence exists supporting the demographic buffering hypothesis (e.g., Gaillard & Yoccoz 2003; Rotella et al. 2012) or not (McDonald et al. 2017). However, generalisation of demographic buffering patterns across species remains challenging for several reasons (Doak *et al.* 2005; Morris & Doak 2004).

One of the challenges surrounding demographic buffering are the different interpretations of results from correlational analyses, as in Pfister (1998) and Hilde *et al.* (2020). Some authors rank species' life histories along a continuum from buffered to labile (see Box 1 for definition) using the correlation coefficient (Spearman’s correlation *ρ*) between the impact of demographic processes on the population growth rate and the temporal variance of said demographic processes (McDonald *et al.* 2017; Salguero-Gómez 2021). There, negative correlation coefficient values indicate demographic buffering. Alternatively, the absence of statistical support for buffering may suggest a preference for demographic variance to track environmental conditions, a phenomenon coined demographic lability (Drake 2005; Hilde *et al.* 2020; Jäkäläniemi *et al.* 2013; Koons *et al.* 2009; Reed & Slade 2012) (Box 1).

Demographic buffering can be measured in different ways (Gascoigne *et al.* 2023a, 2024a; Haridas & Tuljapurkar 2005; Hilde *et al.* 2020). One way to address demographic buffering is based on the ‘penalisation term’ of Tuljapurkar’s approximation (Box 1), the variance-covariance structure (Tuljapurkar 1982). This approach measures how much temporal variability in demographic processes penalises the population relative to the value of its arithmetic population growth rate. This method uses stochastic elasticities (, Haridas & Tuljapurkar 2005) and, as such, explicitly considers temporal variation in demographic processes. We use this method to compare the demographic buffering patterns across species and identify the populations displaying buffering signatures.

A buffered population is one where *λs* is robust to penalty attributable to temporal variation of demographic processes. Assessing the said robustness relies on a *summed* effect of temporal variability. The summed effect of demographic process variability on population growth rate is related to the extent of impact that a demographic process has over *λs* (Haridas & Tuljapurkar 2005). Given so, we might expect for buffered populations — robust to the aforementioned penalty — to exhibit evidence of restricted temporal variability in the most impacting demographic process for *λt*.

To address this prediction, here we propose that, in addition to measuring the for each population, one should also examine the effects of each demographic process within a population’s life cycle on *λt* (*e.g.*, Caswell 1978, 1996, 2001; Ebert 1999; de Kroon et al. 1986). Furthermore, we propose that alongside this step, an analysis of nonlinear selection pressures acting on the temporal variance of each demographic process (Box 1) is essential.

The sign (>0, <0) of the self-second derivatives determines the type of nonlinear selection acting on demographic process temporal variability. Negative values (concave selection, ∩-shaped) reduce temporal variance, characteristic of buffering (Caswell 1996, 2001; Shyu & Caswell 2014). Positive values (convex selection, ∪-shaped) indicate selection forces that amplify the temporal variance, revealing a lack of selection pressures on demographic process variance (Bruijning *et al.* 2020; Caswell 1996, 2001; Le Coeur *et al.* 2022; Koons *et al.* 2009; Shyu & Caswell 2014; Vinton *et al.* 2022).

Here, we show a novel combination of existing demographic methods to test the following hypothesis: buffered species with low summed effect of temporal variability on their fitness should show signatures of concave selection acting to reduce the variance in their most impacting demographic process(es) (see Box 1 for definitions). Concave selection pressures favour features that contribute to reducing temporal variance (Caswell 2001; Shyu & Caswell 2014), thereby enhancing population persistence in the face of environmental stochasticity. We test our hypothesis and demonstrate the applicability and challenges of our framework using 43 populations of 37 mammal species.

**Methods**

**The summed effects of demographic process variability measured by stochastic elasticities**

, hereafter(Pfister 1998; Rotella *et al.* 2012)egral Projection Models (*IPMs*) (Easterling *et al.* 2000; Ellner *et al.* 2016; Gascoigne *et al.* 2023b; Rodríguez-Caro *et al.* 2021; Wang *et al.* 2023)(Caswell 2001; Ellner *et al.* 2016)note that proposed ies(Doak *et al.* 2021; Griffith 2017)Hereafter, win theas its Zuidema & Franco 2001)ose(Franco & Silvertown 2004)

obtain the stochastic elasticities (Haridas & Tuljapurkar 2005) of *λ*s to variabilityThe can be partitioned into two components: i) the sum of stochastic elasticities with respect to variability[[1]](#footnote-1)\* () — assessing how variability in *aij* affects *λs* —and ii) the sum of stochastic elasticities with respect to the arithmetic mean of demographic processes () — assessing the impact of a change in mean values of demographic processes on *λs* (Haridas & Tuljapurkar 2005). A weak (*i.e.,* near zero) summed effect of variability means that the population growth rate is relatively unaffected by the variability in demographic processes (Haridas & Tuljapurkar 2005), and this lack of effect by demographic process variability is consistent with demographic buffering. As such, a summed effect of variability offers a good proxy to evidence demographic buffering (Gascoigne *et al.* 2024b; Haridas & Tuljapurkar 2005) and enables the classification of populations along a continuum.

demographic process *λs*

**Demographic processes, their first- and second-order effects on *λs,* and types of selection on temporal variance**

The following method delves into within-population level by calculating the partial derivatives of *λ1* (obtained by averaging sequential MPMs across the study duration) concerning each separate matrix element *aij* of the MPM ***A*** (Fig. 1B). This step reveals a first-order effect of demographic process variation on fitness — the elasticities of *λ1* to changes in demographic processes. We then evaluate a second-order effect using self-second derivatives of *λ1* for each *aij* (Fig. 1C) (Caswell 1996; Shyu & Caswell 2014).

First- and second-order effects of the variation in demographic processes on fitness are evidence of *average* selection pressures over time (Carslake *et al.* 2008; Caswell 2001; Kajin *et al.* 2023; Shyu & Caswell 2014; Tuljapurkar *et al.* 2023). While elasticities can be considered a proxy for selection gradients (Lande 1982), a second-order effect (measured as a self-second derivative of *λ1* with respect to each demographic process) reveals the type of selection acting on temporal variability of demographic patterns.

A strong first-order effect of variation on fitness implies in a linear relationship between a demographic process and fitness. When linearity is assumed, the self-second derivatives are near zero, which means selection changes the mean of demographic processes, but not their variance (Shyu & Caswell 2014). Nonzero self-second derivatives indicate *nonlinear* relationships between fitness and a demographic process, revealing additional aspects of selection on the variances and covariances of demographic processes (Brodie *et al.* 1995; Carslake *et al.* 2008; Shyu & Caswell 2014). Furthermore, the second-order derivatives measure how sensitive the population growth rate is to temporal autocorrelation of demographic processes.

We argue that the joint interpretation of first- and second-order effects of variation on *λ1* provides the needed platform to address our prediction of demographically buffered populations displaying concave selection pressures. To address our hypothesis, we:

1. Place populations along a continuum defined by values.
2. Identify the demographic processes with highest elasticities for each population.
3. Associate the same demographic processes identified in (2) with negative self-second derivatives, indicating concave selection.

We showcase these steps on an imaginary wolf population (Fig. 1B). In this wolf population, individuals remaining in the fourth stage (MPM element *a4,4*) have the most impact over *λ1*, with the highest elasticity value (Fig. 1B, yellow square). However, Figure 1C reveals a weak second-order effect of element *a4,4* on *λ1*, thus implying a weak selection pressure to reduce *a4,4* temporal variance. A combination of a strong first-order and near zero second-order effects on fitness coincides with a strong linear influence of a change in the mean of *a4,4* on *λ1*. However, in this example, there is no evidence of concave selection on *a4,4*, as we expected based on the positioning of wolf population on the left (unbuffered) side of the variance continuum (Fig. 1A).

We found evidence of concave selection in the fertility of individuals in the second and third stages of the hypothetical wolf species (Fig. 3C, MPM elements *a1,2* and *a1,3* , respectively, large black dots). Both fertility elements in this wolf population reveal low elasticities (Fig. 3B), but highly negative self-second derivatives. Such a pattern coincides with strong concave selection acting to reduce temporal variance in wolves’ second- and third- stage fertilities. These patterns also reveal that temporal autocorrelation in second- and third- stage fertilities affect population fitness. Nonetheless, the absence of concave selection in the fertility of individuals in the fourth stage (Fig. 3C, MPM element *a1,4*, small black dot) might suggests a pattern consistent with senescence.

Although not our primary goal, we briefly introduce steps to evidence demographic lability. Compelling lability evidence requires sufficient data across environments [over time or space; but see Perret et al. (2024)] to construct reaction norms depicting demographic responses to environmental changes (Drake 2005; Koons *et al.* 2009; Morris *et al.* 2008). Non-linear relationships between demographic processes and the environment must be established based on the reaction norms. Demographic processes where an increase in the mean value has a stronger positive impact on population growth rate than the detrimental effect of increased variance need to be identified. The latter condition is only met when the process-environment reaction norms are convex (Drake 2005, Koons *et al*. 2009, Morris *et al*. 2008). However, Barraquand & Yoccoz (2013) show that even with log-concave reaction norms, environmental variability can positively affect population growth under certain conditions, such as constant survival or density-dependent growth. Importantly, species may not be purely buffered or labile some processes may be buffered, others labile, and others insensitive to environmental variability (*e.g.*, Doak *et al*. 2005). Deciphering these patterns is a primary research interest in the field.

**Demographic buffering in mammals: A case study**

We examine the performance of our framework and test the hypothesis, that is that species at the buffered end of the variance continuum display highly negative self-second derivatives for the governing demographic processes. We use 43 MPMs from 37 mammal species (16 species at the within-populations level). Mammals are of special interest in the context of demographic buffering for two reasons: (1) mammalian life histories have been well studied (Beccari *et al.* 2024; Bielby *et al.* 2007; Gillespie 1977; Jones 2011; Stearns 1983) and (2) some of their populations have already been assessed in terms of demographic buffering, particularly for primates (Campos *et al.* 2017; Morris *et al.* 2008, 2011; Reed & Slade 2012; Rotella *et al.* 2012). Together, the well-studied life histories and previous information about the occurrence of buffering in mammals allow us to make accurate predictions and validate the performance of our framework.

We used MPMs (Caswell 2001) from 43 out of 139 studies with mammals available in the COMADRE Animal Matrix Database v.3.0.0 (Salguero-Gómez *et al.* 2016). These 43 populations encompass 37 species from eight taxonomic orders. We carefully selected these MPMs in our analyses because their models contain values of demographic processes () for three or more contiguous time periods, thus allowing us to obtain the stochastic elasticity of each . Although we are aware that not all possible temporal variation in demographic processes may have been expressed within this period, we assumed three or more transitions are enough to provide sufficient variation for population comparison (Compagnoni *et al.* 2023). To mitigate bias in variance estimates, we randomly extracted three MPMs from the existing data for each species (Supplementary Material, Table S1), calculated the mean of these three MPMs, and repeated this process 50 times to obtain estimates of and their corresponding standard errors. A detailed description of the analysed data and their original sources are detailed in Table S1. Finally, we included MPMs of *Homo sapiens* to cross-check our estimates of second-order derivatives, as it is the only mammalian species where these have been calculated (Caswell 1996). The data for *H. sapiens* were gathered from 26 modern populations (Keyfitz & Flieger 1990).

At the within-populations level, we used a subset of 16 populations (including *H. sapiens*) whose MPMs were age-based. We specifically selected these populations because their life cycles can be summarised by two main demographic processes: survival and contribution to the recruitment of new individuals (Caswell 2010; Ebert 1999).

To quantify the variance continuum and calculate for between-populations level comparisons, we followed Tuljapurkar *et al.* (2003) and Haridas & Tuljapurkar (2005). Next, at the within-populations level, we calculated the deterministic elasticities to each demographic process using the *popbio* package (Stubben *et al.* 2020). The self-second derivatives were adapted from *demogR* (Jones 2007) following (Caswell 1996) and applied to the mean MPM of each study. All analyses were performed using R version 4.4.1 (R Core Team 2024).

**Results**

We ranked 43 populations from 37 mammal species into a continuum of variance according to the summed impact of variation in demographic processes on *λs* (Fig. 2). Most of the analysed taxonomic orders were placed on the low or zero variance end of the variance continuum (Fig. 2), coinciding with demographically buffered populations. The smallest contributions of variability in demographic processes (note that ranges from 0 to -1), suggesting buffered populations, were assigned to Primates: northern muriqui (*Brachyteles hyphoxantus*, = -5.31 × 10-5 ± 2.09 × 10-5) (mean ± S.E.) (Fig. 2 silhouette a), mountain gorilla (*Gorilla beringei*, = -1.28 × 10-5 ± 1.32 × 10-5) (Fig. 2 silhouette b), followed by the blue monkey (*Cercopithecus mitis*, = -4.43 × 10-5 ± 1.18 × 10-5) (Fig. 2 silhouette c). The first non-primate species placed near the buffered end of the continuum was the Columbian ground squirrel (*Urocitellus columbianus*, Rodentia, = -3.38 × 10-3 ± 6.96 × 10-4) (Fig. 2 silhouette d). On the other opposite, the species with the highest contribution of variation in demographic processes – placed at the high-variance end of the continuum – was the stoat (*Mustela erminea*, Carnivora, = -0.310 ± 0.0162) (Fig. 2 silhouette e). All the 14 primate populations occupied the buffered side of the variance continuum, with the exception of the Patas monkey (*Erythrocebus patas*, Primates, = -0.0521 ± 5.38 × 10-3) (Fig. 2 silhouette f). The snowshoe hare (*Lepus americanus*, Lagomorpha, = -0.262 ± 0.0233) (Fig. 2 silhouette g) and the Bush rat (*Rattus fuscipes*, Rodentia, = -0.245 ± 4.29 × 10-3) (Fig. 2 silhouette h) were positioned on the non-buffered end of the variance continuum. Additional information (including standard errors of the elasticity estimates) is provided in Table S1. *A posteriori*, we quantified the impact of phylogenetic relatedness on the estimates of the sum of stochastic elasticities (Fig. 2), and then for the correlation between those estimates and the number of MPMs available per species. For the former, we estimated Blomberg’s K, a measure of phylogenetic signal that ranges between 0 (weak signal) to positive values 1 (strong) (Münkemüller *et al.* 2012). Blomberg’s K in our analyses was 0.23. The correlation between the number of available MPMs per study and the sum of stochastic elasticities (post jack-knifing) raised a weakly negative coefficient (-0.002), though significant (P = 0.017).

We found evidence in support of our hypothesis in only one of the studied species, the Columbian ground squirrel (*Urocitellus columbianus*). This species is placed near the buffered end of the variance continuum (Fig. 2, silhouette d) *and* its most impactful demographic process shows signs of concave selection. The strongly negative self-second derivative with respect to growth from first to the second stage (Fig. 3B, MPM element *a2,1*) indicates that *a2,1* is both important, and at the same time, kept constant through time in this population of *U. columbianus*.

the support for our hypothesis was present, but weaker, as humans are placed further away from the buffered end of the variance continuum (Fig. 2, silhouette j). However, the growth and growth from second to third age classsand *a3,2*, respectivelyalongsideD, corroborating with demographically buffered population

For the remaining studied species the demographic processes with the highest elasticity values did not display strong negative self-second derivatives (Fig. 3). Particularly for the majority of primates, placed on the buffered end of the variance continuum, demographic processes with high elasticities had positive values for the self-second derivatives (indicated by yellow squares with white dots in Figure 3). Examples of primate species exhibiting high elasticities and positive values for their self-second derivatives include northern muriqui (*Brachyteles hypoxanthus*), mountain gorilla (*Gorilla beringei*), white-faced capuchin monkey (*Cebus capucinus*), rhesus monkey (*Macaca mulatta*), blue monkey (*Cercopithecus mitis*), Verreaux’s sifaka (*Propithecus verreauxi*) and olive baboon (*Papio cynocephalus*) (Fig. 3). This implies that the key demographic processes influencing *λ1* do not show evidence of selective pressure for reducing their variability.

The killer whale (*Orcinus orca*) showed similar lack of support for our hypothesis as primates. Indeed, *O. orca* was positioned at the buffered end of the variance continuum (Cetacea, = -4.72 × 10-4 ± 1.53 × 10-4) (Fig. 2 silhouette not shown). However, the first- and second-order effects show that the governing three demographic processes in the killer whale life cycle (namely, matrix elements *a2,2*, *a3,3*, and *a4,4*) are not under selection pressures for reducing their temporal variance, but the opposite (yellow and green squares with white dots, Fig. 3).

The primary governing demographic process for Soay sheep (*Ovis aries*) displayed convex selection signatures. For *O. aries* (Fig. 2, silhouette i), remaining in the third age class (Fig. 3, *a3,3*,) impacts *λt* most and is under selection pressure to have its variance increased. These characteristics suggest potential conditions for lability, despite the species being positioned closer to the buffered end of the variance continuum.

Adding the second-order effect of variation on fitness to the toolbox for demographic buffering is an important addition. The high absolute values of self-second derivatives (large dots, either black or white, Fig. 3) suggest *λt* is sensitive to autororrelation in those demographic processes. This pattern also means that if, for example, the mean value of *a5,4* for *U. maritimus* increased, the sensitivity of *λt* to *a5,4* would decrease because the self-second derivative of *a5,4* is highly negative (depicted by the largest black dot in polar bear, Fig. 3 silhouette j). The opposite holds for the *a4,4*, where an increase in the value of *a4,4* would increase the sensitivity of *λt* to *a4,4*, because the self-second derivative of *a4,4* is highly positive (the largest white dot in the polar bear MPM).

**Discussion**

We explore demographic buffering patterns through the integration of established demographic techniques. Our framework merges insights from both stochastic and deterministic demographic approaches, which revealed only limited support for our hypothesis. Specifically, we had anticipated that species exhibiting minimal influence from temporal variability in demographic processes on their stochastic growth rates would demonstrate concave selection affecting the demographic processes with the highest deterministic elasticities. However, using stochastic elasticities alongside the first- and second- order perturbation analysis of the deterministic population growth rate and applying these analyses to mammal species, we found that only the Columbian ground squirrel fully supported our hypothesis; humans showed partial support; other species did not.

Evidencing demographic buffering is not straightforward. Indeed, through the analysis of stochastic population growth rate (*λs*) in our application of the framework to 43 populations of 37 mammal species, we identify the highest density of natural populations near the buffered end of the variance continuum. However, we show that most of the species then fail to exhibit signs of concave (∩-shaped) selection on impacting demographic parameters, opposed to our hypothesis. Such results suggest discordance between two features of demographic buffering, namely: 1) the stochastic population growth rate having a low sensitivity to temporal variability in demographic processes, and 2) demographic processes having their temporal variability reduced by selection.

The lack of association between the non-linear selection patterns (concave/convex) and species positioning on the variance continuum for the studied mammal species may have several explanations. Firstly, non-linear selection on demographic process variability is *dynamic* (Kajin *et al.* 2023). Within a life cycle, even minor changes in key demographic processes can trigger a domino effect, affecting not only the process itself but also the sensitivity of *λ1* to changes in said process (Stearns 1992). Consequently, correlations between demographic processes (negative correlations known as trade-offs) are influenced by minor alterations in the governing demographic processes (Doak *et al.* 2005). Because of these characteristics, second-order derivatives reveal “fine scale” fitness behaviour compared to sums of stochastic elasticities. Evolutionary demography still requires new tools to connect second-order fitness effects with stochastic elasticities in a biologically interpretable manner, similar as in Tuljapurkar *et al.* 2023).

The stochastic elasticities explicitly account for the demographic process variation in time, while the first- and second- order effects on fitness are obtained from temporally averaged population matrices. Because a mean environment rarely characterizes the natural variation in demographic process typical of stochastic environments (Boyce *et al.* 2006), any metric derived from averaged matrix population models represent only an averaged realisation and could only rarely be representative of a pattern emerged from explicitly accounting for temporal variation.

Our original assumptions regarding demographically buffered populations, however, remain valid. We assumed that: 1) a buffered population is one with a weak summed effect of temporal variability on the long-term stochastic population growth rate, and 2) if a population is buffered, there should be signs of concave selection acting on the demographic process with the highest deterministic elasticity. The lack of support for our hypothesis supports the idea that the patterns of first- and second-order effects of demographic process variation on fitness are dynamic and can change rapidly in natural environments. Even if a given demographic process is primarily governing the population growth rate in one year, a different one might take over next year (Evers *et al.* 2021).

When placing our study species along a variance continuum, primates tend to be located on the buffered end. However, most primates displayed convex – instead of the expected concave – selection on adult survival. Similar results, where the key demographic process failed to display reduced temporal variability, have been reported for long-lived seabirds (Doherty *et al.* 2004). One explanation for the unexpected convex selection on adult survival involves trade-offs, as suggested by (Doak *et al.* 2005). When two demographic parameters are negatively correlated, the variance of population growth rate can be increased or decreased (Compagnoni *et al.* 2016; Evans & Holsinger 2012).

Correlations among demographic processes (positive and negative) inherently influence the biological limits of variance (Haridas & Tuljapurkar 2005). This is because the magnitude of variation in a particular demographic process is restrained by the variation of other demographic processes. Not surprisingly, correlations among demographic processes have been shown to be strongly subjected to ecological factors (Fay *et al.* 2022). Therefore, future studies may benefit from deeper insights using *cross*-second derivatives (Caswell 1996, 2001) to investigate correlations among demographic processes.

Biological variance estimates are inevitably subjected to several sources of bias (Simmonds & Jones 2024). To minimise bias, we randomly sampled the available matrices before obtaining the estimates. Despite the significant correlation between and the number of available matrices per species, the relative positioning of species remains meaningful for between-population level comparisons, as the correlation is very weak (-0.002). Still, researchers carrying out macroecological comparisons of demographic buffering might want to be even more stringent than we have been here with their datasets, as these grow longer with time (Compagnoni *et al.* 2021; Salguero-Gómez *et al.* 2021).

Regarding phylogenetic effects, our tests revealed a mild signal, but we note that future work regressing values against potential independent variables (*e.g.*, climate values) may want to correct for this phylogenetic dependence.By having carefully chosen studies from a database that contains >400 species and retained only those that passed through a set of selection criteria (Che-Castaldo *et al.* 2020; Gascoigne *et al.* 2023b; Kendall *et al.* 2019; Römer *et al.* 2024; Simmonds & Jones 2024), we mitigate those biases *a priori*. Furthermore, we are using an elasticity-based approach, meaning we are comparing proportional variances. At present, the available methods still do not account for constraints in variance nor performing a perturbation approach disproportionately.

The analyses at both between- and within-populations levels are fundamentally interconnected. This connection is grounded on the fact that large summed elasticities to variability are intrinsically linked to high elasticity values, as demonstrated in equation 6 in (Haridas & Tuljapurkar 2005). This finding robustly endorses the perspective that species' positions along the variance continuum should be interpreted with consideration of first and second-order effects, and additionally, in the context of selection pressures acting on the variability of demographic processes, as revealed by second-order derivatives.

Demographic processes within our study populations often face a mix of convex and concave selection. This mix of selection patterns was suggested by Doak et al. (2005), who noted that dramatic changes in population growth rate sensitivities are influenced by correlations among demographic processes. Here, only two of the 16 mammal species revealed concave selection on the key demographic processes: Columbian ground squirrel (*Urocitellus columbianus*), and humans (*Homo sapiens*). These two species were placed near (or relatively near) the buffered end of the variance continuum, supporting (partially) our hypothesis. Evidence of buffering has been reported across 22 ungulate species (Gaillard & Yoccoz 2003). However, in the one ungulate we examined, the moose (*Alces alces*), we found only partial support for our hypothesis, as it is near the buffered end of the variance continuum but lacks concave selection pressures on the most important demographic process.

Our overall findings reveal varying levels of support for the notion that adult survival in long-lived species tends to be buffered. Indeed, Gaillard et al. (1998) found that adult female survival varied considerably less than juvenile survival in large herbivores. This finding was also supported by further studies in ungulates (Gaillard & Yoccoz 2003), turtles (Heppell 1998), vertebrates and plants (Pfister 1998), and more recently across nine species of plants (McDonald *et al.* 2017). Gaillard and Yoccoz (2003) reported unexpectedly high adult survival in small mammals, even though the studied small mammals were annual, and as such, comparable to large mammal model. Seasonality, frequency and method of sampling all influence survival estimates and their estimated variability, thus, when comparing multiple species/studies, all the latter characteristics should be taken into account when interpreting the results.

Examining the drivers of demographic buffering has become an important piece of the ecological and evolutionary puzzle of demography. As such, understanding buffering can help us better predict population responses to environmental variability, climate change, and direct anthropogenic disturbances (Boyce *et al.* 2006; Gascoigne *et al.* 2024a; McDonald *et al.* 2017; Pfister 1998; Vázquez *et al.* 2017). By setting demographic buffering into a broader and more integrated frameworks, we hope to enhance comprehension and prediction of the implications of heightened environmental stochasticity on the evolution of life history traits. This understanding is crucial in mitigating the risk of extinction for the most vulnerable species.

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**Data availability** The demographic data used in this paper are open-access and available in the COMADRE Animal Matrix Database (https://compadre-db.org/Data/Comadre). A list of the studies and species used here is available in Supplementary Material (Table S1). The data and code supporting the results can be accessed here: https://github.com/SamuelGascoigne/Demographic\_buffering\_

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**Figure 1**

A diagram of a dinosaur

Description automatically generated

**Figure 2**

**A graph with images of animals

Description automatically generated**

**Figure 3**

**A screenshot of a graph

Description automatically generated**

**Figure legends**

**Figure 1**. A) The variance continuum for 37 hypothetical species based on the summed stochastic elasticities () at the between populations hierarchical level. The closer the is to zero, the weaker the impact of variation in demographic processes on the stochastic population growth rate, *λs*. The variance continuum ranges from potentially buffered (right-hand side) to less buffered (left-hand side) populations. The yellow-dotted populations can be classified as having potentially *buffered life cycles*. The left-hand side of the graph represents populations where variability in demographic processes results in strong impact on *λs* (blue dots). Thus, the blue-dotted populations can be classified as having potentially *unbuffered life cycles*. The vertical axis delineates the values of the probability density function, indicating the frequency of populations at each value of . The placement of data points (species/populations) along the horizontal axis corresponds to their calculated values of and is arranged linearly, while the placement along the y-axis is random for improved visual comprehension. B) First-order effects or elasticities for separate populations at within-species level. Shown are the elasticities of the deterministic population growth rate (*λ1*) for a hypothetical population of wolves and revealing the most important demographic process(es) in the life cycle (yellow cells: high elasticity, blue cells: low elasticity). C) Combined results for first- (yellow and blue cells) and second-order effects (black dots), where the latter reveals the nonlinear selection pressures at the within-species level.

**Figure 2**. The variance continuum for 43 populations from 37 species of mammals from the COMADRE database based on the summed stochastic elasticities of *λs* to temporal variability in demographic processes () at the between-populations hierarchical level. Colors represent different taxonomic orders with Primates occupying the right-hand side. Silhouettes: a) *Brachyteles hyphoxantus*, b) *Gorilla beringhei*, c) *Cercopithecus mitis*, d) *Urocitellus columbianus,* e) *Mustela erminea*, f) *Erythrocebus patas*, g) *Lepus americanus*, h) *Rattus fuscipes*, i) *Ovis aries*, j) *Homo sapiens*, k) *Macropus eugenii*, and l) *Felis catus*. The vertical axis delineates the values of the probability density function, indicating the frequency of populations at each value of . The placement of data points (species/populations) along the horizontal axis corresponds to their calculated values of and is arranged linearly, while the placement along the y-axis is random for improved visual comprehension.

**Figure 3:** First- and second-order effects on population growth rate, *λ1* (corresponding to elasticities and self-second derivatives of population growth rate, respectively) for 16 mammal species. The 16 plots represent populations where the MPMs built by ages were available in the COMADRE Animal Matrix Database. The yellow-blue colour scale represents elasticity values for each of the demographic processes in the MPM, where yellow cells represent high and blue cells low elasticity of deterministic population growth rate to changes in demographic processes. No colour means elasticity=0. The black dots represent negative self-second derivatives of *λ1* - corresponding to concave selection - and the white dots represent positive self-second derivatives of *λ1* - ditto convex selection. The dot sizes are scaled by the absolute value of self-second derivatives, where the smaller the dot, the closer a self-second derivative is to 0, indicating weak or no nonlinearity. Thus, large dots indicate strong nonlinear selection forces, either concave (black) or convex (white). Since the derivatives of population growth rate are confounded by eigen-structure (Kroon *et al.* 2000), the scaling of the elasticity values and second-derivative values is species specific - *i.e.*, each plot has its own scale. Species-specific scales can be found in Supplementary material (Table S2).

BOX 1:

**The demographic buffering hypothesis**: Stemming from Tuljapurkar’s approximation (Tuljapurkar 1982), Pfister (1998) showed that the penalisation term representing the variance-covariance structure, tends to be reduced when elasticities of demographic processes and their coefficients of variation covary negatively. However, the term demographic buffering was only coined later(*sensu* Morris & Doak 2004).The demographic buffering hypothesis is also referred to as “adaptive buffering” (*sensu* Le Coeur et al. 2022), suggesting that *selection* acts to minimize the negative impacts of environmental variation by reducing the temporal variance of key demographic processes (*e.g.*, survival, development, reproduction) that have the highest sensitivity/elasticity to population growth rate, a fitness proxy (Gaillard & Yoccoz 2003; Pfister 1998).

**Demographic buffering** is a broader concept than the demographic buffering hypothesis; it refers to a population's capacity to withstand environmental variability by keeping essential demographic processes stable over time (Gascoigne *et al.* 2024a, b; Hilde *et al.* 2020; Morris & Doak 2004; Pfister 1998). It is worth noting that this term does not explicit allude to the evolutionary mechanisms that include selection, which are predicted by the demographic buffering hypothesis (Le Coeur *et al.* 2022)*.*

**Demographic lability**: A population's ability to accommodate fluctuations in demographic processes in response to temporal variations in environmental conditions (Le Coeur *et al.* 2022; Jäkäläniemi *et al.* 2013; Koons *et al.* 2009). The relationship between the labile demographic process and the environment can be convex, concave, or linear. A labile vital rate in a variable environment will have an average value that is greater than, less than, or equal to the vital rate estimated in the mean environment, depending on the shape of the relationship. Similar as for the demographic buffering hypothesis, the demographic lability hypothesis relies on *selection* for demographic process to track environmental fluctuations in a way that increases the long-term fitness (*λs*). This process occurs when the increase in demographic process mean — due to convexity — overcomes the detrimental effect of temporal variance in annual population growth rates (Le Coeur *et al.* 2022).

**Sensitivity**: Represented by a first-order partial derivative of population growth rate with respect to each demographic process (Caswell 1978, 2001; Ebert 1999), sensitivity measures the absolute change in fitness that a change in a demographic process would cause.

**Elasticity**: Proportional sensitivity. A measure of proportional change in fitness caused by a proportional change in demographic process. Elasticities can be of different types (Grant *et al.* 2007; Haridas *et al.* 2009; Haridas & Tuljapurkar 2005, 2007; de Kroon *et al.* 1986; Kroon *et al.* 2000; Van Tienderen 2000; Tuljapurkar *et al.* 2003) and with respect to both, the stochastic and the deterministic population growth rates.

**Tuljapurkar’s approximation**: To overcome dealing with complex probability distributions that describe demographic fluctuations through time, the approximation captures the essence of the effect of temporal variability, at least for small amounts of variability (*i.e.* small noise). It states that the logarithm of the long-term stochastic population growth rate equals the geometric mean growth rate plus a penalty term containing the demographic process variance-covariance structure (Tuljapurkar 1982).

**Supplementary material – Data available in COMADRE Version 3.0.0 and results from Step 1 of the framework**

**Table S1.** The metadata used and the respective results presented in the main text. The first four columns represent the information from where Matrix Populations Models (MPMs) were extract precisely as presented in COMADRE 3.0.0.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Species** | **Common name** | **Species (COMADRE)** | **Order** | **# matrices** |  |  |  | **(SE)** |
| *Homo sapiens sapiens* | Human | Homo\_sapiens\_subsp.\_sapiens | Primates | 26 | 1.063707 | 1.061537 | -2.24E-03 | 3.15E-04 |
| *Alces alces* | Moose | Alces\_alces | Artiodactyla | 14 | 1.205368 | 1.205161 | -6.69E-04 | 8.42E-05 |
| Antechinus agilis | Agile antechinus | Antechinus\_agilis | Dasyuromorphia | 3 | 0.931076 | 0.885919 | -1.11E-01 | 1.62E-03 |
| Bos primigenius | Cattle | Bos\_primigenius | Artiodactyla | 8 | 1.002505 | 1.000493 | -2.83E-03 | 2.96E-04 |
| Brachyteles hypoxanthus | Northern muriqui | Brachyteles\_hypoxanthus | Primates | 25 | 1.05122 | 1.051273 | -5.31E-05 | 2.09E-05 |
| Callospermophilus lateralis | Golden-mantled ground squirrel | Callospermophilus\_lateralis | Rodentia | 18 | 2.052345 | 1.970253 | -6.68E-02 | 8.72E-03 |
| Cebus capucinus | White faced capuchin monkey | Cebus\_capucinus | Primates | 22 | 1.020887 | 1.020868 | -2.04E-04 | 4.75E-05 |
| Cercopithecus mitis | Blue monkey | Cercopithecus\_mitis | Primates | 28 | 1.036082 | 1.036075 | -4.43E-05 | 1.18E-05 |
| Cervus canadensis subsp. nelsoni | Rocky Mountain elk | Cervus\_canadensis\_subsp.\_nelsoni | Artiodactyla | 10 | 1.107412 | 1.099838 | -8.55E-03 | 1.09E-03 |
| Eumetopias jubatus | Northern sea lion; Steller sea lion | Eumetopias\_jubatus | Carnivora | 4 | 0.904383 | 0.902155 | -4.52E-03 | 2.44E-04 |
| Felis catus | Feral cat | Felis\_catus | Carnivora | 3 | 1.948471 | 1.8259 | -1.34E-01 | 1.89E-03 |
| Gorilla beringei | Mountain gorilla | Gorilla\_beringei | Primates | 41 | 1.026827 | 1.02682 | -1.28E-05 | 1.32E-05 |
| Hippocamelus bisulcus | Huemul deer | Hippocamelus\_bisulcus | Artiodactyla | 3 | 0.996197 | 0.995462 | -1.80E-03 | 1.09E-04 |
| Leopardus pardalis | Ocelot | Leopardus\_pardalis | Carnivora | 4 | 1.086146 | 1.086122 | -2.94E-04 | 3.89E-05 |
| Lepus americanus | Snowshoe hare | Lepus\_americanus | Lagomorpha | 5 | 0.811904 | 0.707678 | -2.62E-01 | 2.33E-02 |
| Lycaon pictus | African wild dog | Lycaon\_pictus | Carnivora | 3 | 1.500429 | 1.430517 | -9.70E-02 | 9.91E-04 |
| Macaca mulatta | Rhesus macaque | Macaca\_mulatta\_3 | Primates | 24 | 1.127496 | 1.12735 | -3.84E-04 | 6.83E-05 |
| Macropus eugenii | Tammar wallaby | Macropus\_eugenii | Diprotodontia | 15 | 0.981097 | 0.970794 | -1.43E-02 | 1.62E-03 |
| Marmota flaviventris | Yellow-bellied marmot | Marmota\_flaviventris\_2 | Rodentia | 8 | 0.89031 | 0.886098 | -8.80E-03 | 6.98E-04 |
| Marmota flaviventris | Yellow-bellied marmot | Marmota\_flaviventris\_3 | Rodentia | 8 | 0.920541 | 0.916392 | -7.00E-03 | 7.04E-04 |
| Microtus oeconomus | Root vole | Microtus\_oeconomus | Rodentia | 28 | 1.027531 | 1.027095 | -5.60E-04 | 1.06E-04 |
| Mustela erminea | Stoat | Mustela\_erminea | Carnivora | 4 | 1.258462 | 1.074391 | -3.10E-01 | 1.62E-02 |
| Orcinus orca | Killer whale | Orcinus\_orca\_2 | Cetacea | 50 | 0.998658 | 0.998351 | -4.72E-04 | 1.53E-04 |
| Ovis aries | Soay sheep | Ovis\_aries\_2 | Artiodactyla | 6 | 1.09877 | 1.080656 | -3.45E-02 | 2.96E-03 |
| Pan troglodytes subsp. schweinfurthii | Eastern chimpanzee | Pan\_troglodytes\_subsp.\_schweinfurthii | Primates | 45 | 0.982286 | 0.982191 | -1.94E-04 | 5.06E-05 |
| Papio cynocephalus | Olive baboon | Papio\_cynocephalus | Primates | 37 | 1.053872 | 1.053789 | -2.41E-04 | 6.97E-05 |
| Peromyscus maniculatus | Deer mouse | Peromyscus\_maniculatus\_2 | Rodentia | 4 | 1.10686 | 1.101117 | -9.41E-03 | 6.88E-04 |
| Phascolarctos cinereus | Koala | Phascolarctos\_cinereus\_2 | Diprotodontia | 4 | 1.064011 | 1.062744 | -2.53E-03 | 2.16E-04 |
| Phocarctos hookeri | New Zealand sea lion | Phocarctos\_hookeri | Carnivora | 16 | 1.023016 | 1.020083 | -3.56E-03 | 4.15E-04 |
| Propithecus verreauxi | Verreaux's sifaka | Propithecus\_verreauxi | Primates | 24 | 0.985592 | 0.985399 | -3.06E-04 | 6.29E-05 |
| Rattus fuscipes | Bush rat | Rattus\_fuscipes | Rodentia | 3 | 1.304662 | 1.188931 | -2.45E-01 | 4.29E-03 |
| Urocitellus armatus | Uinta ground squirrel | Spermophilus\_armatus | Rodentia | 6 | 1.125011 | 1.113416 | -1.73E-02 | 1.68E-03 |
| Urocitellus armatus | Uinta ground squirrel | Spermophilus\_armatus\_2 | Rodentia | 6 | 1.094693 | 1.084304 | -1.47E-02 | 1.56E-03 |
| Urocitellus columbianus | Columbian ground squirrel | Spermophilus\_columbianus | Rodentia | 6 | 1.008949 | 0.984575 | -3.80E-02 | 3.26E-03 |
| Urocitellus columbianus | Columbian ground squirrel | Spermophilus\_columbianus\_3 | Rodentia | 6 | 1.200353 | 1.197473 | -3.38E-03 | 6.96E-04 |
| Ursus americanus subsp. floridanus | Florida black bear | Ursus\_americanus\_subsp.\_floridanus | Carnivora | 4 | 1.01989 | 1.018094 | -3.68E-03 | 3.97E-04 |
| Ursus arctos subsp. horribilis | Grizzly bear | Ursus\_arctos\_subsp.\_horribilis\_5 | Carnivora | 7 | 1.025712 | 1.024785 | -1.38E-03 | 1.26E-04 |
| Ursus maritimus | Polar bear | Ursus\_maritimus\_2 | Carnivora | 5 | 0.940646 | 0.931697 | -1.91E-02 | 9.23E-04 |
| Brachyteles hypoxanthus | Northern muriqui | Brachyteles\_hypoxanthus\_2 | Primates | 25 | 1.110953 | 1.110983 | 1.22E-05 | 5.05E-06 |
| Cebus capucinus | White-faced capuchin monkey | Cebus\_capucinus\_2 | Primates | 22 | 1.059311 | 1.059248 | -1.03E-04 | 2.85E-05 |
| Chlorocebus aethiops | Vervet | Chlorocebus\_aethiops\_2 | Primates | 8 | 1.187136 | 1.148862 | -8.03E-02 | 1.31E-02 |
| Erythrocebus patas | Patas monkey | Erythrocebus\_patas | Primates | 9 | 1.127974 | 1.092178 | -5.21E-02 | 5.38E-03 |
| Gorilla beringei subsp. beringei | Mountain gorilla | Gorilla\_beringei\_subsp.\_beringei | Primates | 41 | 1.052588 | 1.05255 | -6.81E-05 | 1.11E-05 |

**Table S2**. The species-specific scales for the elasticity of *λ1* to changes in demographic processes and for the self-second derivatives of *λ1* with respect to demographic processes for the 16 mammal species studied.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Figure 3 reference | Species common name | Emin=elasticity minimum value | Emax=elasticity maximum value | SSDmin=self-second derivative minimum value | SSDmax=self-second derivative maximum value |
| A | Blue monkey | 0 | 0.52 | -1.25 | 1.27 |
| B | Columbian ground squirrel | 0 | 0.23 | -1.48 | 0.01 |
| C | Eastern chimpanzee | 0 | 0.60 | -4.39 | 2.59 |
| D | Human | 0 | 0.18 | -0.15 | 0.08 |
| E | Killer whale | 0 | 0.55 | -5.72 | 3.43 |
| F | Moose | 0 | 0.55 | -0.66 | 0.36 |
| G | Mountain gorilla | 0 | 0.81 | -1.46 | 0.28 |
| H | Northern muriqui | 0 | 0.72 | -1.17 | 0.35 |
| I | Olive baboon | 0 | 0.54 | -0.57 | 1.13 |
| J | Polar bear | 0 | 0.26 | -0.73 | 0.54 |
| K | Rhesus macaque | 0 | 0.51 | -0.54 | 0.71 |
| L | Root vole | 0 | 0.86 | -2.54 | 0.22 |
| M | Soay sheep | 0 | 0.56 | -0.22 | 0.40 |
| N | Tammar wallaby | 0 | 0.55 | -0.64 | 0.34 |
| O | Verreaux’s sifaka | 0 | 0.60 | -2.64 | 1.34 |
| P | White faced capuchin monkey | 0 | 0.66 | -2.66 | 1.21 |

1. Standard deviation (σ) stands for a measure of variability. [↑](#footnote-ref-1)