

A unified framework to quantify demographic buffering in natural populations

Gabriel Santos¹, Samuel Gascoigne², André Dias³, Maja Kajin², and Roberto Salguero-Gomez²

¹National Institute of the Atlantic Forest (INMA)

²University of Oxford

³Universidade Federal do Rio de Janeiro

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Abstract

The Demographic Buffering Hypothesis (DBH) predicts that natural selection reduces the temporal fluctuations in demographic processes (such as survival, development, and reproduction), due to their negative impacts on population dynamics. However, a comprehensive approach that allows for the examination of demographic buffering patterns across multiple species is still lacking. Here, we propose a three-step framework aimed at quantifying demographic buffering. Firstly, we categorize species along a continuum of variance based on the sums of stochastic elasticities. Secondly, we examine the linear selection gradients, followed by the examination of nonlinear selection gradients as the third step. With these three steps, our framework overcomes existing limitations of conventional approaches to quantify demographic buffering, allows for multi-species comparisons, and offers insight into the evolutionary forces that shape demographic buffering. We apply this framework to mammal species and discuss both the advantages and potential of our framework.

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5 Gabriel Silva Santos^{1,2*}, Samuel J L Gascoigne^{3*}, André Tavares Corrêa Dias⁴, Maja Kajin
6 ^{3,5**♦}, Roberto Salguero-Gómez^{3♦}

7
8 1 National Institute of the Atlantic Forest (INMA), 29650-000, Santa Teresa, Espírito Santo,
9 Brazil. ssantos.gabriel@gmail.com

10 2 Department of Ecology, Graduate Program in Ecology and Evolution, Rio de Janeiro
11 State University, 524 São Francisco Xavier Street, 20550-900, Maracanã, Rio de Janeiro,
12 Brazil

13 3 Department of Biology, University of Oxford, South Parks Road, OX1 3RB, Oxford, UK.
14 samuel.gascoigne@pmb.ox.ac.uk, rob.salguero@biology.ox.ac.uk,
15 maja.kajin@biology.ox.ac.uk

16 4 Department of Ecology, Institute of Biology, Universidade Federal do Rio de Janeiro,
17 Avenida Carlos Chagas Filho 373, 21941-590 Rio de Janeiro, RJ, Brazil. atcdias@gmail.com

18 5 Department of Biology, Biotechnical Faculty, University of Ljubljana, Večna pot 111, 1000
19 Ljubljana, Slovenia

20
21 *Shared first authorship

22 **Corresponding author

23 ♦Shared senior authorship

24
25 AUTHOR CONTRIBUTIONS: GSS developed the initial concept, performed the statistical
26 analyses, and contributed to the first draft of the manuscript. SJLG developed the initial
27 concept, contributed to the first draft and all other versions of the manuscript, and generated
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50 **Abstract** (143/150 words)

51 The Demographic Buffering Hypothesis (DBH) predicts that natural selection reduces the
52 temporal fluctuations in demographic processes (such as survival, development, and
53 reproduction), due to their negative impacts on population dynamics. However, a
54 comprehensive approach that allows for the examination of demographic buffering patterns
55 across multiple species is still lacking. Here, we propose a three-step framework aimed at
56 quantifying demographic buffering. Firstly, we categorize species along a continuum of
57 variance based on the sums of stochastic elasticities. Secondly, we examine the linear
58 selection gradients, followed by the examination of nonlinear selection gradients as the third
59 step. With these three steps, our framework overcomes existing limitations of conventional
60 approaches to quantify demographic buffering, allows for multi-species comparisons, and
61 offers insight into the evolutionary forces that shape demographic buffering. We apply this
62 framework to mammal species and discuss both the advantages and potential of our
63 framework.

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67 Environmental stochasticity shapes organisms' life histories (Bonsall & Klug 2011).
68 Nonetheless, how organisms will cope with the increasing variation in environmental
69 conditions (Boyce *et al.* 2006; Morris *et al.* 2008) remains an intriguing ecological and
70 evolutionary question (Sutherland *et al.* 2013). Evolutionary demography provides diverse
71 explanations for how evolutionary processes shape demographic responses to environmental
72 stochasticity (Charlesworth 1994; Healy *et al.* 2019; Hilde *et al.* 2020; Pfister 1998;
73 Tuljapurkar *et al.* 2009). The long-term stochastic population growth rate, expressed as the
74 geometric mean of annual growth rates (Tuljapurkar 1982), forms the basis of the
75 Demographic Buffering Hypothesis (DBH) (Morris & Doak 2004; Pélabon *et al.* 2020).

76 Increasing the geometric mean of λ corresponds to a rise in the long-term stochastic
77 population growth rate (λ_s , hereafter). Conversely, higher variance in λ reduces λ_s (Morris &
78 Doak 2004; Tuljapurkar 1982), impacting population persistence. The DBH predicts that life
79 histories are under selection pressure to minimise the negative impacts of environmental
80 variation by constraining the temporal variance of those demographic processes (*e.g.*,
81 survival, development, reproduction) to which population growth rate (*i.e.*, fitness) is most
82 sensitive to (Gaillard & Yoccoz 2003; Pfister 1998). The *demographic pattern* operating the
83 DBH, *i.e.*, demographic buffering, describes the selection-driven constraint on the temporal
84 variance of the most impacting demographic processes for the population growth rate (Hilde
85 *et al.* 2020; Morris & Doak 2004; Pfister 1998). Here, we focus on the latter - on the
86 emerging pattern of demographic buffering in different animal life histories – rather than on
87 the DBH itself.

88 A unified approach to unambiguously quantify demographic buffering is still missing.
89 Indeed, identifying demographic buffering remains challenging (Doak *et al.* 2005; Morris &
90 Doak 2004) for several reasons, one of them being different interpretation of results from
91 correlational analyses (*e.g.*, as in Pfister, 1998). Some authors rank species' life histories on a

92 continuum from buffered to labile using the correlation coefficient (Spearman's correlation
93 ρ), where negative values indicate buffering (McDonald *et al.* 2017). Alternatively, the
94 absence of statistical support for buffering may suggest a preference for demographic
95 variance to track environmental conditions, known as the Demographic Lability Hypothesis
96 (DLH) (Hilde *et al.* 2020; Jäkäläniemi *et al.* 2013; Koons *et al.* 2009; Reed & Slade 2012).
97 However, increased temporal variance alone is not enough to constitute demographic lability;
98 it must also result in significant changes in the mean value of the demographic process (Le
99 Coeur *et al.* 2022).

100 Another obstacle to achieving generalization across species' populations regarding
101 demographic buffering is the typical hierarchical level of examination. Some studies focus on
102 characteristics drawn from the *entire population model (between-populations level)*
103 (McDonald *et al.* 2017; Reed & Slade 2012). At this level, a life history is considered
104 demographically buffered if key demographic processes have low temporal variance (Le
105 Coeur *et al.* 2022; Hilde *et al.* 2020; Morris & Doak 2004; Pfister 1998). However, to fully
106 grasp how and why demographic buffering occurs, and how patterns might change in
107 response to the environment, we must also consider characteristics at the level of separate
108 *components of population model (within-populations level)*. Within a population, one
109 demographic process may be buffered while another may be labile (Barraquand & Yoccoz
110 2013; Jongejans *et al.* 2010; Koons *et al.* 2009). Thus far, studies have focused on either one
111 of the hierarchical levels, however, for a mechanistic understanding of how environmental
112 stochasticity shapes life histories, both between- and within-population levels need to be
113 addressed at the same time.

114 The complexity of examining the underlying mechanisms of demographic buffering
115 presents additional challenge. Evidence suggests buffering in both long-lived (Doak *et al.*
116 2005; Gaillard & Yoccoz 2003; McDonald *et al.* 2017; Pfister 1998; Rotella *et al.* 2012), and

117 short-lived species (Ferreira *et al.* 2013; Pfister 1998; Reed & Slade 2012). However, these
118 patterns alone do not fully reveal how life histories are shaped by natural selection. First-
119 order effects, such as elasticities, show how variation in demographic processes affects
120 population growth rate, while second-order effects reveal sensitivity to autocorrelation
121 (Tuljapurkar 1990). Integrating both allows a better understanding of fitness function
122 behaviour near local maxima and minima.

123 In linear relationships between fitness and demographic processes, second-order
124 derivatives of population growth rate are zero, indicating natural selection acts on mean
125 values (Shyu & Caswell 2014). Nonzero second derivatives suggest nonlinear relationships
126 between fitness and a demographic process, revealing additional aspects of selection on the
127 variances and covariances of demographic processes (Brodie *et al.* 1995; Carslake *et al.*
128 2008; Shyu & Caswell 2014). The sign (>0 , $=0$, <0) of the self-second derivative of λ with
129 respect to demographic processes determines the type of selection. Negative values describe
130 concave (\cap -shaped) selection, reducing temporal variance (Caswell 1996, 2001; Shyu &
131 Caswell 2014) and thus, indicating demographic buffering. Positive values indicate convex
132 (\cup -shaped) selection, amplifying variance (Caswell 1996, 2001; Shyu & Caswell 2014) and
133 potentially indicating demographic lability (Le Coeur *et al.* 2022; Koons *et al.* 2009). To
134 confirm lability, increased variance must shift the mean value of a demographic process,
135 outweighing its negative effect on population growth rate (Le Coeur *et al.* 2022).

136 The diverse demographic strategies across species result from evolutionary processes
137 shaping variance in demographic processes over time. Integrating demographic buffering into
138 the context of linear and nonlinear selection enables quantification of the evolutionary forces
139 driving these patterns, shedding light on how environmental variability shapes existing and
140 novel strategies. Despite this, a unified approach to characterize demographic buffering
141 signatures remains lacking.

142 Here, we introduce a framework to quantify demographic buffering, offering insight
143 into temporal variance patterns affected by environmental stochasticity. This framework
144 involves categorizing species or populations along a variance continuum based on the degree
145 of natural selection buffering key demographic processes, with three steps incorporating well-
146 known methods applied to stage-structured demographic data (*e.g.*, matrix population models
147 [Caswell 2001]; integral projection models [(Easterling et al. 2000)]. First, species or
148 populations are positioned on the continuum to assess cumulative effects of variance in
149 demographic processes on population growth rate. Second, linear selection forces within the
150 life cycle of each species or population are investigated at the within-populations level. Third,
151 non-linear selection forces within the life cycle are explored at the within-populations level.
152 These steps provide quantitative evidence of demographic buffering occurrence. Lastly,
153 further analyses are proposed to identify demographic lability.

154 To demonstrate the applicability of our framework, we apply it to 40 populations of
155 34 mammal species sourced from the COMADRE database (Salguero-Gómez *et al.* 2016).
156 We showcase how the framework can provide valuable insights into the patterns of
157 demographic buffering across species. The framework offers novel, detailed insights into the
158 selection pressures that act within species' life cycles, thus allowing for a thorough
159 understanding of the evolutionary selection forces that shape the patterns of demographic
160 buffering across species. Beyond providing a quantitative, systematic toolset to quantify
161 buffering through three steps, we have also offered an alternative fourth step that briefly
162 outlines how to evidence lability.

163

164 **A unified framework to assess evidence of demographic buffering**

165 The evidence for demographic buffering has been mainly assessed using Matrix Population
166 Models (MPM; Pfister 1998; Rotella et al. 2012)). However, Integral Projection Models

167 (IPM; Rodríguez-Caro et al. 2020; Wang et al. 2023) can be equally applied for identifying
168 the demographic buffering signatures. Both MPMs and IPMs are stage-structured, discrete-
169 time demographic models (Caswell 2001; Ellner *et al.* 2016). For simplicity, here we focus
170 on MPMs, but note that the same approaches are as equally applicable to IPMs (Doak *et al.*
171 2021; Griffith 2017). Throughout this manuscript, we refer to demographic processes as both
172 matrix entries a_{ij} (*i.e.*, upper-level parameters) and the vital rates that underlie the matrix
173 elements (*i.e.*, lower-level parameters), and note that their conversion is straightforward and
174 described elsewhere (Franco & Silvertown 2004). The framework operates on three steps.
175 In the first step of our framework, we calculate the impact of variation in demographic
176 processes on the stochastic growth rate, λ_s , known as stochastic elasticities E_{ij}^S (Haridas &
177 Tuljapurkar 2005) (Figure 1A). This calculation separates the sum of all stochastic elasticities
178 ($\Sigma E_{a_{ij}}^S$) into two components: one for assessing how temporal variance affects λ_s ($\Sigma E_{a_{ij}}^{S\sigma}$), and
179 the other for assessing the impact of mean values of demographic processes on λ_s , ($\Sigma E_{a_{ij}}^{S\mu}$)
180 (Haridas & Tuljapurkar 2005). A higher absolute value of the sum of stochastic elasticity
181 with respect to variance ($\Sigma E_{a_{ij}}^{S\sigma}$), indicates greater sensitivity of λ_s to changes in demographic
182 process variance, suggesting absence of buffering. Conversely, a lower absolute value
183 suggests demographic buffering, where λ_s is less sensitive to such perturbations (Haridas &
184 Tuljapurkar 2005; Tuljapurkar *et al.* 2003) (Fig. 1A). This step places species or populations
185 along a continuum based on variance in demographic processes, with unconstrained variance
186 on the left (possibly unbuffered) and constrained variance on the right (possibly buffered).
187 However, unconstrained variance does not necessarily imply demographic lability, defined as
188 an increase in *mean value* of a demographic process in response to improved environmental
189 conditions (Le Coeur *et al.* 2022). By examining $\Sigma E_{a_{ij}}^{S\sigma}$, we can assess changes in the
190 contribution of demographic process variance to λ_s , while mean values remain unchanged.

191 Although this step provides insight into how environmental variation affects λ_s , it does not
192 consider covariances between demographic processes and serial correlations, which are
193 important for fully diagnosing buffering (Haridas & Tuljapurkar 2005). Instead, our approach
194 focuses on second derivatives of population growth rate with respect to demographic
195 processes to elucidate selection's impact on variance (step 3, below).

196 Steps 2 and 3 of the framework delve into within-population analysis. After step 1
197 positions species or populations along the variance continuum for λ_s , each life cycle
198 undergoes scrutiny. Step 2 (Fig. 1B) involves calculating the partial derivatives of λ_t
199 concerning all matrix elements of the MPM. This step reveals how each demographic process
200 influences λ_t . In step 3, one evaluates nonlinear selection patterns using self-second
201 derivatives of λ_t for each demographic process (Fig. 1C). This step unveils potential nonlinear
202 selection pressures on demographic processes, crucial for understanding their evolutionary
203 dynamics. Failure to consider these evolutionary processes in step 1 may lead to
204 misinterpretation of patterns (*e.g.*, Lawler et al. 2009).

205 Steps 2 and 3 of the framework analyse averaged selection pressures over time
206 periods. They offer insights into how perturbations in demographic processes affect λ_t ,
207 obtained by averaging sequential Matrix Population Models (MPMs) across the study
208 duration. Therefore, they enhance our understanding of selection pressures' role in shaping
209 demographic patterns across various species.

210 In step 3, it is important to note that the importance of demographic processes shifts
211 with changing environments (Stearns 1992). This dynamic sensitivity of λ_t to specific
212 processes (Kroon *et al.* 2000), indicated by self-second derivatives, helps pinpoint which
213 processes are most likely to induce changes. For instance, in the hypothetical wolf species
214 (Fig. 1), a decline in reproduction among third age-class individuals (matrix element $a_{1,3}$)
215 would heighten sensitivity to that process. Consequently, with increased environmental

216 variability, the key demographic process might change from remaining in the fourth age class
217 (matrix element $a_{4,4}$, Fig. 1B) to reproduction of the third age-class (matrix element $a_{1,3}$, Fig.
218 1C).

219 Combining the three steps of our framework allows for a quantitative identification of
220 buffering. Steps 2 and 3 offer key insights as to *why* a given species or population is placed
221 on either the buffered or the non-buffered end of the variance continuum. A clear and
222 unequivocal evidence for support towards buffering consists of: (1) a species or population
223 being positioned near the 0 end of the continuum (the right-hand side) in step 1; (2) this
224 species' or populations' life cycle having one or more demographic processes with highest
225 elasticity values in step 2; and (3) the same demographic process displaying the highest
226 elasticity in step 2 with negative self-second derivative values in step 3. In this sense, Figure
227 1B shows that, for the chosen population of a hypothetical wolf species, the most important
228 demographic process is remaining in the fourth stage (MPM element $a_{4,4}$), as this
229 demographic process results in highest elasticity value (Fig. 1B yellow square). However,
230 Fig. 1C reveals that $a_{4,4}$ is under little selection pressure for variance reduction. Thus, there is
231 no clear evidence of buffering from the third step of the framework (*i.e.*, no concave selection
232 forces). This way, the lack of concave selection forces on the key demographic process
233 within wolf's life cycle explains why this species is placed on the left-hand side of the
234 variance continuum (Fig. 1A).

235 Although not our primary goal here, we briefly introduce said step 4. To establish
236 compelling evidence of lability, it is essential to fulfil several further criteria. First, sufficient
237 data across various environments (over time or space) are required to construct reaction
238 norms that depict how a demographic process responds to environmental changes (Koons *et*
239 *al.* 2009; Morris *et al.* 2008), which can be challenging in terms of sufficient and high-quality
240 demographic and environmental data. Second, non-linear relationships between demographic

241 processes and the environment must be established based on the demographic process-
242 environment reaction norms. Lastly, demographic processes where an increase in the mean
243 value has a stronger positive impact on population growth rate than the detrimental effect of
244 increased variance needs to be identified. The latter condition is only met when the
245 demographic process-environment reaction norm takes a convex shape (resembling a "U"
246 shape), as described by Koons et al. (2009) and Morris et al. (2008). However, a study by
247 Barraquand & Yoccoz (2013) reported diverging results in this regard. Importantly, we note
248 that more likely than previously thought (*e.g.*, Pfister 1998), species do not exist as purely
249 buffering or labile, but that within populations, some vital rates may be buffered, other labile,
250 and others insensitive to the environment (*e.g.*, Doak et al. 2005). Deciphering generality in
251 this likely complex pattern should attract much research attention going forward, in our
252 opinion.

253

254 **Demographic buffering in mammals: a case study using the unified framework**

255 We demonstrate the performance of our framework using 44 MPMs from 34 mammal
256 species. Mammals are of special interest here for two reasons: (1) mammalian life histories
257 have been well studied (Bielby *et al.* 2007; Gillespie 1977; Jones 2011; Stearns 1983); and
258 (2) some of their populations have already been assessed in terms of buffering, particularly
259 for primates (Campos *et al.* 2017; Morris *et al.* 2008, 2011; Reed & Slade 2012; Rotella *et al.*
260 2012). Together, the well-studied life histories and previous information about the occurrence
261 of buffering in mammals provide the necessary information to make accurate predictions and
262 validate the performance of the proposed framework.

263 We used Matrix Population Models from 40 out of 139 studies with mammals
264 available in the COMADRE database v.3.0.0 (Salguero-Gómez *et al.* 2016). These 40
265 populations encompass 34 species from eight taxonomic orders. We included these MPMs in
266 our analyses because they provide values of demographic processes (a_{ij}) for three or more

267 contiguous time periods, thus allowing us to obtain the stochastic elasticity of each a_{ij} .
268 Although we are aware that not all possible temporal variation in demographic processes may
269 have been expressed within this period, we assumed three or more transitions are enough to
270 provide sufficient variation for population comparison. At least three contiguous time periods
271 - a common selection criteria in comparative studies of stochastic demography (Compagnoni
272 *et al.* 2023) - also allowed to test and showcase our framework. Fortunately, several long-
273 lived species, characterized by low variation in their demographic processes, were studied for
274 a long time (*e.g.*, some primates in our dataset have been studied for over 20 years – Morris
275 *et al.* 2011). We removed the populations where either only survival or only reproduction
276 rates were reported, because of the impossibility to calculate the stochastic growth rate. A
277 detailed description of the analysed data and their original sources are available in
278 supplementary material (Supplementary Material, Table S1).

279 *Homo sapiens* was included in our analyses because it is the only mammalian species
280 in which second-order derivatives have been applied (Caswell 1996). Therefore, *Homo*
281 *sapiens* provides an ideal basis for comparisons among species. The data for *Homo sapiens*
282 were gathered from 26 modern populations located in various cities, allowing us to construct
283 a spatiotemporal variance. It is important to note that in this case, we are not working with
284 true temporal variance but rather a variance that encompasses both spatial and temporal
285 aspects.

286 For steps 2 and 3 of our framework, we utilized a subset of 16 populations (including
287 *Homo sapiens*) whose population projection matrices (MPMs) were organized by age. We
288 specifically selected these populations because their life cycles can be summarized by two
289 main demographic processes: survival and contribution to recruitment of new individuals.
290 The contribution to recruitment can be interpreted as either the mean reproductive output for
291 each age class or an approximation thereof, depending on how the matrices are structured

292 (Ebert 1999). One advantage of using such matrices is that they encompass only two types of
293 demographic processes, namely survival and recruitment, eliminating the need to account for
294 multiple transitions between different life stages.

295 To perform the step 1 of our framework and obtain the $\Sigma E_{a_{ij}}^{S\sigma}$ (and $\Sigma E_{a_{ij}}^{S\mu}$), we followed
296 Tuljapurkar et al. (2003) and Haridas & Tuljapurkar (2005). To perform step 2 of our
297 framework, we calculated the deterministic elasticities of each demographic process extracted
298 using the *popbio* package. All analyses were performed using R version 3.5.1 (R Core team,
299 2018). Finally, to perform the step 3 of our framework the self-second derivatives were
300 adapted from *demogR* (Jones 2007) following (Caswell 1996) and applied for the mean
301 MPM.

302 *Results*

303 We ranked 40 populations from the 34 identified mammal species according to the
304 cumulative impact of variation in demographic processes on λ_s using the step 1 of our
305 framework (Fig. 2). Additional information (including standard deviations of the elasticity
306 estimates and number of matrices available) is provided in the supplementary material (Table
307 S1). Most of the analysed orders were placed on the low-variance end of the variance
308 continuum (Fig. 2). The smallest contributions of variation in demographic processes (*i.e.*,
309 maximum value of $\Sigma E_{a_{ij}}^{S\sigma}$, note that $\Sigma E_{a_{ij}}^{S\sigma}$ ranges from 0 to -1), suggesting more buffered
310 populations, were assigned to Primates: northern muriqui (*Brachyteles hypoxantus*, $\Sigma E_{a_{ij}}^{S\sigma} = -$
311 $0.09 \times 10^{-4} \pm 0.12 \times 10^{-4}$) (mean \pm standard deviation) (Fig. 2 silhouette a), mountain gorilla
312 (*Gorilla beringhei*, $\Sigma E_{a_{ij}}^{S\sigma} = -0.24 \times 10^{-4} \pm 0.08 \times 10^{-4}$) (Fig. 2 silhouette b), followed by the
313 blue monkey (*Cercopithecus mitis*, $\Sigma E_{a_{ij}}^{S\sigma} = -0.63 \times 10^{-4} \pm 0.06 \times 10^{-4}$) (Fig. 2 silhouette c).
314 The first non-primate species placed near the low-variance end of the continuum was the
315 Columbian ground squirrel (*Urocitellus columbianus*, Rodentia, $\Sigma E_{a_{ij}}^{S\sigma} = -0.003 \pm 0.002$) (Fig.

316 2 silhouette d). The species with the highest contribution of variation in demographic
317 processes placed at the high-variance end of the continuum was the stoat (*Mustela erminea*,
318 Carnivora, $\Sigma E_{a_{ij}}^{S\sigma} = -0.35 \pm 0.02$) (Fig. 2 silhouette e). All the 14 primate populations
319 displayed potential evidence of buffering, occupying the right-hand side of the variance
320 continuum, with the exception of the Patas monkey (*Erythrocebus patas*, Primates, $\Sigma E_{a_{ij}}^{S\sigma} = -$
321 0.05 ± 0.03) (Fig. 2 silhouette f). The snowshoe hare (*Lepus americanus*, Lagomorpha, $\Sigma E_{a_{ij}}^{S\sigma}$
322 $= -0.29 \pm 0.16$) (Fig. 2 silhouette g) and the Bush rat (*Rattus fuscipes*, Rodentia, $\Sigma E_{a_{ij}}^{S\sigma} = -0.25$
323 ± 0.03) (Fig. 2 silhouette h) appear on the high-variance end of the continuum.

324 As predicted for the steps 2 and 3, we could not observe a clear pattern in support of
325 buffering. This finding means that the demographic processes with the highest elasticity
326 values failed to display strongly negative self-second derivatives (Fig. 3). Particularly for
327 majority of primates - with the lack or minor temporal variation in demographic processes -
328 demographic processes with high elasticities had positive values for the self-second
329 derivatives (indicated by yellow squares with white dots in Fig. 3). Examples of primate
330 species exhibiting high elasticities and positive values for the self-second derivatives and
331 include northern muriqui (*Brachyteles hypoxanthus*), mountain gorilla (*Gorilla beringei*),
332 white-faced capuchin monkey (*Cebus capucinus*), rhesus monkey (*Macaca mulatta*), blue
333 monkey (*Cercopithecus mitis*), Verreaux's sifaka (*Propithecus verreauxi*) and olive baboon
334 (*Papio cynocephalus*) (Fig. 3). This implies that the key demographic processes influencing
335 λ_t are not subject to selective pressure for reducing their temporal variability. However, even
336 though the primates were positioned closer to the low-variance end of the continuum in step
337 1, the evidence from steps 2 and 3 does not support the occurrence of buffering in the most
338 influential demographic processes.

339 The killer whale showed similar controversy between step 1 and steps 2-3 results as
340 most primates. In step 1, the killer whale was positioned at the buffered end of the variance
341 continuum (*Orcinus orca*, Cetacea, $\Sigma E_{a_{ij}}^{S\sigma} = -0.70 \times 10^{-4} \pm 1.04 \times 10^{-5}$) (Fig. 2 silhouette not
342 shown). However, steps 2 and 3 show that the three demographic processes in killer whale
343 life cycle with highest elasticity values (matrix elements $a_{2,2}$, $a_{3,3}$ and $a_{4,4}$) are not under
344 selection pressures for reducing their temporal variance, but the opposite (depicted by yellow
345 and green squares with white dots, Fig. 3).

346 The only primate species exhibiting evidence of buffering in steps 2 and 3 was
347 human. In human, demographic parameters representing survival from first to second age
348 class (matrix element $a_{2,1}$) displayed high elasticities and negative self-second derivatives
349 (depicted as yellow squares with black dots in Fig. 3). Evidence supporting buffering was
350 also found in the Columbian ground squirrel (*Urocitellus columbianus*), where, similar to
351 humans, survival from the first to the second age class (matrix element $a_{2,1}$) showed
352 indications of selection acting to reduce $a_{2,1}$ variance. Accordingly, the Columbian ground
353 squirrel was positioned close to the buffered end of the variance continuum in step 1. Hence,
354 the Columbian ground squirrel was the sole species with consistent evidence of buffering
355 across all three steps of the framework.

356 The Soay sheep (*Ovis aries*) was the species furthest from the buffered end of the
357 variance continuum that enabled to perform steps 2 and 3. For the Soay sheep, remaining in
358 the third age class (matrix element $a_{3,3}$) has the major influence on λ_t and is under selection
359 pressure to have its variance increased. The latter characteristics reveal potential conditions
360 for lability even though the species is placed closer to the buffered end of the variance
361 continuum.

362 Steps 2 and 3 illustrate the importance of examining buffering evidence on the within-
363 populations level. These two steps of the framework identify the simultaneous acting of
364 concave and convex selection on different demographic processes within a single life cycle.
365 In polar bear (*Ursus maritimus*), the key demographic process (matrix element $a_{4,4}$) is under
366 convex selection, as depicted by a yellow square with a white dot in Fig. 3. However, the
367 demographic process with the second highest elasticity value (matrix element $a_{5,4}$) is under
368 strong concave selection (depicted by a light green square with a black dot in Fig. 3).

369 By adding step 3 to the framework, another important information was accessed. The
370 high absolute values of self-second derivatives (large dots, either black or white, Fig. 3)
371 indicate where the sensitivity of λ_t to demographic parameters is itself prone to environmental
372 changes. For instance, if the value of $a_{5,4}$ for polar bear increased, the sensitivity of λ_t to $a_{5,4}$
373 would decrease because the self-second derivative of $a_{5,4}$ is highly negative (depicted by the
374 largest black dot in polar bear MPM). Vice versa holds for the $a_{4,4}$ demographic process,
375 where an increase in the value of $a_{4,4}$ would increase λ_t 's sensitivity to $a_{4,4}$, because the self-
376 second derivative of $a_{5,4}$ is highly positive (depicted by the largest white dot in polar bear
377 MPM). Thus, sensitivities (or equally elasticities) of demographic processes with high
378 absolute values for self-second derivatives can easily change.

379

380 **Discussion**

381 In the Anthropocene, identifying and quantifying mechanisms of species responses to
382 stochastic environments holds crucial importance. This importance is particularly tangible in
383 the context of the unprecedented environmental changes and uncertainties that impact the
384 dynamics and persistence of natural populations (Boyce *et al.* 2006). Correlational
385 demographic analysis, whereby the importance of demographic processes and their temporal
386 variability is examined (Pfister 1998), has attempted to identify how species may buffer

387 against the negative effects of environmental stochasticity. However, these widely used
388 approaches have important limitations (see Introduction and Hilde *et al.* 2020). One
389 significant limitation is the issue of measurement scale concerning demographic processes
390 (Hilde *et al.* 2020; Morris & Doak 2004). Demographic processes, such as birth rates, death
391 rates, immigration, and emigration, operate at various temporal and spatial scales. The choice
392 of scale at which these processes are measured can impact the outcomes of correlational
393 demographic analysis (Bjørkvoll *et al.* 2016). Our novel framework overcomes said
394 limitations by providing a rigorous approach to quantify demographic buffering (Hilde *et al.*
395 2020; Pfister 1998).

396 Evidencing demographic buffering is not straightforward. Indeed, through the
397 analysis of stochastic population growth rate (λ_s) in our application of the framework to 44
398 populations of 34 species, we identify the highest density of natural populations near the
399 buffered end of the variance continuum (step 1). However, we show that the same species
400 then fail to exhibit signs of concave (\cap -shaped) selection on the key demographic parameters
401 when further analyses are performed averaging the variation across the duration of each study
402 (steps 2 and 3). This finding confirms that placing the species near the buffered end of the
403 variance continuum is *necessary* but not *sufficient* to diagnose demographic buffering.
404 Indeed, buffering occurs when concave selection forces act on the key demographic
405 parameter (Caswell 1996, 2001; Shyu & Caswell 2014).

406 Combining the three steps into a unified framework is of utmost importance. In steps
407 2 and 3 of the framework, we find relatively limited overall evidence of buffering in the
408 examination of our 16 (out of 34 in step 1) studied animal species. Step 3 of our framework
409 reveals that the role of natural selection shaping temporal variation in demographic processes
410 is more complex than expected. Indeed, demographic processes within our study populations
411 are often under a mix of convex and concave selection. This mix of selection patterns was

412 already suggested by Doak *et al.* (2005). Here, only two out of 16 mammal species revealed
413 concave selection acting on the key demographic processes (Columbian ground squirrel
414 [*Uroditellus columbianus*], and humans, [*Homo sapiens sapiens*]). These two species were
415 also placed near the buffered end of the variance continuum, therefore meeting all the
416 necessary conditions to diagnose buffering. However, finding 12.5% (two out of 16) species
417 that meet the criteria for demographic buffering is not in concordance with previous studies.
418 Evidence of buffering has been reported across 22 ungulate species (Gaillard & Yoccoz
419 2003). In the one ungulate we examined, the moose (*Alces alces*), we find only partial
420 support for buffering in adult survival, since this species is placed near the buffered end of
421 the variance continuum in step 1 but does not show concave selection pressures on adult
422 survival in step 2/3, as would be necessary to confirm the occurrence of buffering.

423 It is worth noting that a varying number of matrices per species were employed,
424 ranging from 1 to 21, with an average of 8.1 matrices per species (as shown in Table S1).
425 Naturally, having a greater number of matrices is preferred in such analyses. Furthermore,
426 while the size of matrices (matrix dimensions) does not directly bias the results of our
427 framework in any way – since steps 2 and 3 are shown for all the demographic processes
428 independent of matrix dimension – potential implications of varying matrix dimensions
429 should be further investigated in the future.

430 Our overall findings reveal varying levels of support for the notion that adult survival
431 in long-lived species tends to be buffered. Indeed, (Gaillard *et al.* 1998) found that adult
432 female survival varied considerably less than juvenile survival in large herbivores. This
433 finding was also supported by further studies in ungulates and small rodents (Gaillard &
434 Yoccoz 2003), turtles (Heppell 1998), vertebrates and plants (Pfister 1998), and more
435 recently across nine (out of 73) species of plants (McDonald *et al.* 2017).

436 When placing our study species along a variance continuum (step 1), primates tend to
437 be located on the buffered end. However, most primates displayed convex –instead of the
438 expected concave– selection on adult survival. Similar results, where the key demographic
439 process failed to display constrained temporal variability, have been reported for long-lived
440 seabirds (Doherty *et al.* 2004). One explanation for the unexpected convex selection on adult
441 survival involves trade-offs, as suggested by (Doak *et al.* 2005). When two demographic
442 parameters are negatively correlated, the variance of population growth rate (λ) can be
443 increased or decreased (Compagnoni *et al.* 2016; Evans & Holsinger 2012). The well-
444 established trade-off between survival and fecundity (Roff & Fairbairn 2007; Stearns 1992)
445 might explain the observed deviation of our results. Because variation in primate recruitment
446 is already constrained by physiological limitations (Campos *et al.* 2017), when adult survival
447 and recruitment are engaged in a trade-off, this trade-off might lead to our unexpected result.
448 Correlations among demographic processes (positive and negative) inherently influence the
449 biological limits of variance (Haridas & Tuljapurkar, 2005). This is because the magnitude of
450 variation in a particular demographic process is constrained by (the variation of) other
451 demographic processes that exert an influence on it. Not surprisingly, correlations among
452 demographic processes have been shown to be strongly subjected to ecological factors (Fay
453 *et al.* 2022). Here, future studies may benefit from deeper insights via cross-second
454 derivatives (Caswell 1996, 2001) to investigate correlations among demographic processes.

455 Examining the drivers of demographic buffering has become an important piece of the
456 ecological and evolutionary puzzle of demography. As such, quantifying buffering can help
457 us better predict population responses to environmental variability, climate change, and direct
458 anthropogenic disturbances (Boyce *et al.* 2006; McDonald *et al.* 2017; Pfister 1998; Vázquez
459 *et al.* 2017). By setting demographic buffering into a broader and integrated framework, we
460 hope to enhance comprehension and prediction of the implications of heightened

461 environmental stochasticity on the evolution of life history traits. This understanding is
462 crucial in mitigating the risk of extinction for the most vulnerable species.

463

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470

471 **Data availability**

472 The demographic data used in this paper are open-access and available in the COMADRE
473 Animal Matrix Database (<https://compadre-db.org/Data/Comadre>). A list of the studies and
474 species used here is available in Supplementary Material (Table S1). The data and code
475 supporting the results can be accessed here:

476 https://github.com/SamuelGascoigne/Demographic_buffering_unified_framework.

477

478 **References**

- 479 Barraquand, F. & Yoccoz, N.G. (2013). When can environmental variability benefit
480 population growth? Counterintuitive effects of nonlinearities in vital rates. *Theor Popul*
481 *Biol*, 89, 1–11.
- 482 Bielby, J., Mace, G.M., Bininda-Emonds, O.R.P., Cardillo, M., Gittleman, J.L., Jones, K.E.,
483 *et al.* (2007). The Fast-Slow Continuum in Mammalian Life History: An Empirical
484 Reevaluation. *Am Nat*, 169, 748–757.
- 485 Bjørkvoll, E., Lee, A.M., Grøtan, V., Saether, B.-E., Stien, A., Engen, S., *et al.* (2016).
486 Demographic buffering of life histories? Implications of the choice of measurement
487 scale. *Ecology*, 97, 40–47.
- 488 Bonsall, M.B. & Klug, H. (2011). The evolution of parental care in stochastic environments.
489 *J Evol Biol*, 24, 645–655.

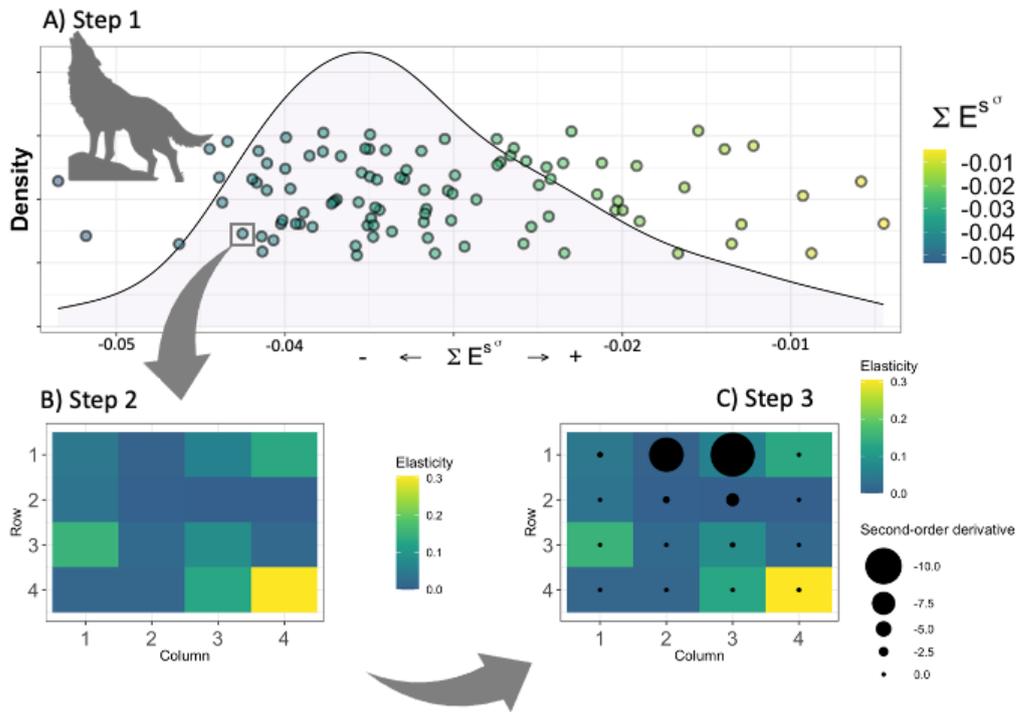
- 490 Boyce, M.S., Haridas, C. V., Lee, C.T., Boggs, C.L., Bruna, E.M., Coulson, T., *et al.* (2006).
491 Demography in an increasingly variable world. *Trends Ecol Evol*, 21, 141–148.
- 492 Brodie, E.I., Moore, A. & Janzen, F. (1995). Visualizing and quantifying natural selection.
493 *Trends Ecol Evol*, 10, 313–318.
- 494 Campos, F.A., Morris, W.F., Alberts, S.C., Altmann, J., Brockman, D.K., Cords, M., *et al.*
495 (2017). Does climate variability influence the demography of wild primates? Evidence
496 from long-term life-history data in seven species. *Glob Chang Biol*, 23, 4907–4921.
- 497 Carslake, D., Townley, S. & Hodgson, D.J. (2008). Nonlinearity in eigenvalue-perturbation
498 curves of simulated population projection matrices. *Theor Popul Biol*, 73, 498–505.
- 499 Caswell, H. (1996). Second Derivatives of Population Growth Rate: Calculation and
500 Applications. *Ecology*, 77, 870–879.
- 501 Caswell, H. (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*.
502 Sinauer Associates Inc. Publishers, Sunderland, Massachusetts, USA.
- 503 Charlesworth, B. (1994). *Evolution in age-structured populations*. second edi. Cambridge
504 University Press.
- 505 Le Coeur, C., Yoccoz, N.G., Salguero-Gómez, R. & Vindenes, Y. (2022). Life history
506 adaptations to fluctuating environments: Combined effects of demographic buffering
507 and lability. *Ecol Lett*, 1–13.
- 508 Compagnoni, A., Bibian, A.J., Ochocki, B.M., Rogers, H.S., Schultz, E.L., Sneek, M.E., *et al.*
509 (2016). The effect of demographic correlations on the stochastic population dynamics
510 of perennial plants. *Ecol Monogr*, 86, 480–494.
- 511 Compagnoni, A., Evers, S. & Knight, T. (2023). Spatial replication can best advance our
512 understanding of population responses to climate. *bioRxiv*,
513 <https://doi.org/10.1101/2022.06.24.497542>.
- 514 Doak, D.F., Morris, W.F., Pfister, C., Kendall, B.E. & Bruna, E.M. (2005). Correctly
515 Estimating How Environmental Stochasticity Influences Fitness and Population Growth.
516 *Am Nat*, 166, E14–E21.
- 517 Doak, D.F., Waddle, E., Langendorf, R.E., Louthan, A.M., Isabelle Chardon, N., Dibner,
518 R.R., *et al.* (2021). A critical comparison of integral projection and matrix projection
519 models for demographic analysis. *Ecol Monogr*, 91, e01447.
- 520 Doherty, P.F., Schreiber, E.A., Nichols, J.D., Hines, J.E., Link, W.A., Schenk, G.A., *et al.*
521 (2004). Testing life history predictions in a long-lived seabird: A population matrix
522 approach with improved parameter estimation. *Oikos*, 105, 606–618.
- 523 Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000). Size-Specific Sensitivity: Applying a
524 New Structured Population Model. *Ecology*, 81, 694–708.
- 525 Ebert, T. (1999). *Plant and animal populations: Methods in demography*. Academic Press,
526 San Diego, CA, USA.

- 527 Ellner, S.P., Childs, D.Z. & Rees, M. (2016). *Data-driven Modelling of Structured*
528 *Populations. A practical guide to the Integral Projection Model*. Lecture Notes on
529 Mathematical Modelling in the Life Sciences. Springer International Publishing, Cham.
- 530 Evans, M.E.K. & Holsinger, K.E. (2012). Estimating covariation between vital rates : A
531 simulation study of connected vs . separate generalized linear mixed models (GLMMs).
532 *Theor Popul Biol*, 82, 299–306.
- 533 Fay, R., Hamel, S., van de Pol, M., Gaillard, J.M., Yoccoz, N.G., Acker, P., *et al.* (2022).
534 Temporal correlations among demographic parameters are ubiquitous but highly
535 variable across species. *Ecol Lett*, 25, 1640–1654.
- 536 Ferreira, M., Kajin, M., Vieira, M., Zangrandi, P., Cerqueira, R. & Gentile, R. (2013). Life
537 history of a neotropical marsupial: Evaluating potential contributions of survival and
538 reproduction to population growth rate. *Mamm Biol*, 78, 406–411.
- 539 Franco, M. & Silvertown, J. (2004). A comparative demography of plants based upon
540 elasticities of vital rates. *Ecology*, 85, 531–538.
- 541 Gaillard, J.M., Festa-Bianchet, M. & Yoccoz, N.G. (1998). Population dynamics of large
542 herbivores: Variable recruitment with constant adult survival. *Trends Ecol Evol*, 13, 58–
543 63.
- 544 Gaillard, J.-M. & Yoccoz, N. (2003). Temporal Variation in Survival of Mammals: a Case of
545 Environmental Canalization? *Ecology*, 84, 3294–3306.
- 546 Gillespie, J.H. (1977). Natural Selection for Variances in Offspring Numbers: A New
547 Evolutionary Principle. *Am Nat*, 111, 1010–1014.
- 548 Griffith, A.B. (2017). Perturbation approaches for integral projection models. *Oikos*, 126,
549 1675–1686.
- 550 Haridas, C. V. & Tuljapurkar, S. (2005). Elasticities in variable environments: Properties and
551 implications. *American Naturalist*, 166, 481–495.
- 552 Healy, K., Ezard, T.H.G., Jones, O.R., Salguero-Gómez, R. & Buckley, Y.M. (2019). Animal
553 life history is shaped by the pace of life and the distribution of age-specific mortality and
554 reproduction. *Nat Ecol Evol*, 3, 1217–1224.
- 555 Heppell, S.S. (1998). Application of Life-History Theory and Population Model Analysis to
556 Turtle Conservation. *Copeia*, 1998, 367.
- 557 Hilde, C.H., Gamelon, M., Sæther, B.-E., Gaillard, J.-M., Yoccoz, N.G. & Pélabon, C.
558 (2020). The Demographic Buffering Hypothesis: Evidence and Challenges. *Trends Ecol*
559 *Evol*, 35, 523–538.
- 560 Jäkäläniemi, A., Ramula, S. & Tuomi, J. (2013). Variability of important vital rates
561 challenges the demographic buffering hypothesis. *Evol Ecol*, 27, 533–545.
- 562 Jones, J.H. (2007). demogR: A Package for the Construction and Analysis of Age-structured
563 Demographic Models in R. *J Stat Softw*, 22, 1–28.

- 564 Jones, J.H. (2011). Primates and the evolution of long, slow life histories. *Current Biology*,
565 21, R708–R717.
- 566 Jongejans, E., De Kroon, H., Tuljapurkar, S. & Shea, K. (2010). Plant populations track
567 rather than buffer climate fluctuations. *Ecol Lett*, 13, 736–743.
- 568 Koons, D.N., Pavard, S., Baudisch, A. & Jessica E. Metcalf, C. (2009). Is life-history
569 buffering or lability adaptive in stochastic environments? *Oikos*, 118, 972–980.
- 570 Kroon, H. De, Groenendael, J. Van & Ehrlen, J. (2000). Elasticities: A review of methods
571 and model limitations. *Ecology*, 81, 607–618.
- 572 Lawler, R.R., Caswell, H., Richard, A.F., Ratsirarson, J., Dewar, R.E. & Schwartz, M.
573 (2009). Demography of Verreaux’s sifaka in a stochastic rainfall environment.
574 *Oecologia*, 161, 491–504.
- 575 McDonald, J.L., Franco, M., Townley, S., Ezard, T.H.G., Jelbert, K. & Hodgson, D.J. (2017).
576 Divergent demographic strategies of plants in variable environments. *Nat Ecol Evol*, 1,
577 0029.
- 578 Morris, W.F., Altmann, J., Brockman, D.K., Cords, M., Fedigan, L.M., Pusey, A.E., *et al.*
579 (2011). Low Demographic Variability in Wild Primate Populations: Fitness Impacts of
580 Variation, Covariation, and Serial Correlation in Vital Rates. *Am Nat*, 177, E14–E28.
- 581 Morris, W.F. & Doak, D.F. (2004). Buffering of Life Histories against Environmental
582 Stochasticity: Accounting for a Spurious Correlation between the Variabilities of Vital
583 Rates and Their Contributions to Fitness. *Am Nat*, 163, 579–590.
- 584 Morris, W.F., Pfister, C.A., Tuljapurkar, S., Haridas, C. V., Boggs, C.L., Boyce, M.S., *et al.*
585 (2008). Longevity can buffer plant and animal populations against changing climatic
586 variability. *Ecology*, 89, 19–25.
- 587 Pélabon, C., Hilde, C.H., Einum, S. & Gamelon, M. (2020). On the use of the coefficient of
588 variation to quantify and compare trait variation. *Evol Lett*, 4, 180–188.
- 589 Pfister, C. (1998). Patterns of variance in stage-structured populations: Evolutionary
590 predictions and ecological implications. *Proceedings of the National Academy of*
591 *Sciences*, 95, 213–218.
- 592 Reed, A.W. & Slade, N.A. (2012). Buffering and plasticity in vital rates of oldfield rodents.
593 *Journal of Animal Ecology*, 81, 953–959.
- 594 Rodríguez-Caro, R.C., Capdevila, P., Graciá, E., Barbosa, J.M., Giménez, A. & Salguero-
595 Gómez, R. (2020). The demographic buffering strategy has a threshold of effectiveness
596 to increases in environmental stochasticity. *bioRxiv*, 1–41.
- 597 Roff, D.A. & Fairbairn, D.J. (2007). The evolution of trade-offs: Where are we? *J Evol Biol*,
598 20, 433–447.
- 599 Rotella, J.J., Link, W.A., Chambert, T., Stauffer, G.E. & Garrott, R.A. (2012). Evaluating the
600 demographic buffering hypothesis with vital rates estimated for Weddell seals from 30
601 years of mark – recapture data, 162–173.

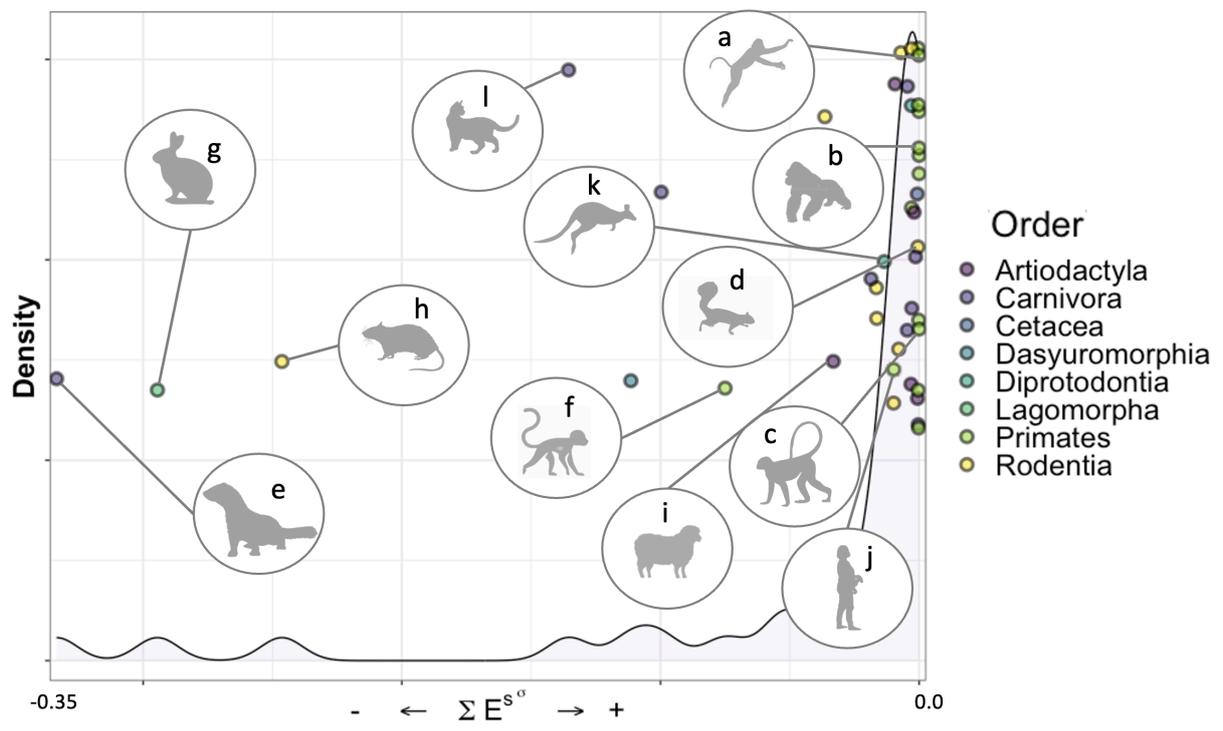
- 602 Salguero-Gómez, R., Jones, O.R., Archer, C.R., Bein, C., de Buhr, H., Farack, C., *et al.*
603 (2016). COMADRE: A global data base of animal demography. *Journal of Animal*
604 *Ecology*, 85, 371–384.
- 605 Shyu, E. & Caswell, H. (2014). Calculating second derivatives of population growth rates for
606 ecology and evolution. *Methods Ecol Evol*, 5, 473–482.
- 607 Stearns, S. (1992). *The Evolution of Life Histories*. Oxford University Press, New York,
608 USA.
- 609 Stearns, S.C. (1983). The Influence of Size and Phylogeny on Patterns of Covariation among
610 Life-History Traits in the Mammals. *Oikos*, 41, 173.
- 611 Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron,
612 D.D., *et al.* (2013). Identification of 100 fundamental ecological questions. *Journal of*
613 *Ecology*, 101, 58–67.
- 614 Tuljapurkar, S. (1990). Population Dynamics in Variable Environments. In: *Lecture notes in*
615 *Biomathematics*, Lecture Notes in Biomathematics (ed. Levin, S.). Springer Berlin
616 Heidelberg.
- 617 Tuljapurkar, S., Gaillard, J.-M. & Coulson, T. (2009). From stochastic environments to life
618 histories and back. *Philosophical Transactions of the Royal Society B: Biological*
619 *Sciences*, 364, 1499–1509.
- 620 Tuljapurkar, S., Horvitz, C.C. & Pascarella, J.B. (2003). The Many Growth Rates and
621 Elasticities of Populations in Random Environments. *Am Nat*, 162, 489–502.
- 622 Tuljapurkar, S.D. (1982). Population dynamics in variable environments. III. Evolutionary
623 dynamics of r-selection. *Theor Popul Biol*, 21, 141–165.
- 624 Vázquez, D.P., Gianoli, E., Morris, W.F. & Bozinovic, F. (2017). Ecological and
625 evolutionary impacts of changing climatic variability. *Biological Reviews*, 92, 22–42.
- 626 Wang, J., Yang, X., Silva Santos, G., Ning, H., Li, T., Zhao, W., *et al.* (2023). Flexible
627 demographic strategies promote the population persistence of a pioneer conifer tree
628 (*Pinus massoniana*) in ecological restoration. *For Ecol Manage*, 529, 120727.
- 629
- 630

631 **Figure 1**



632

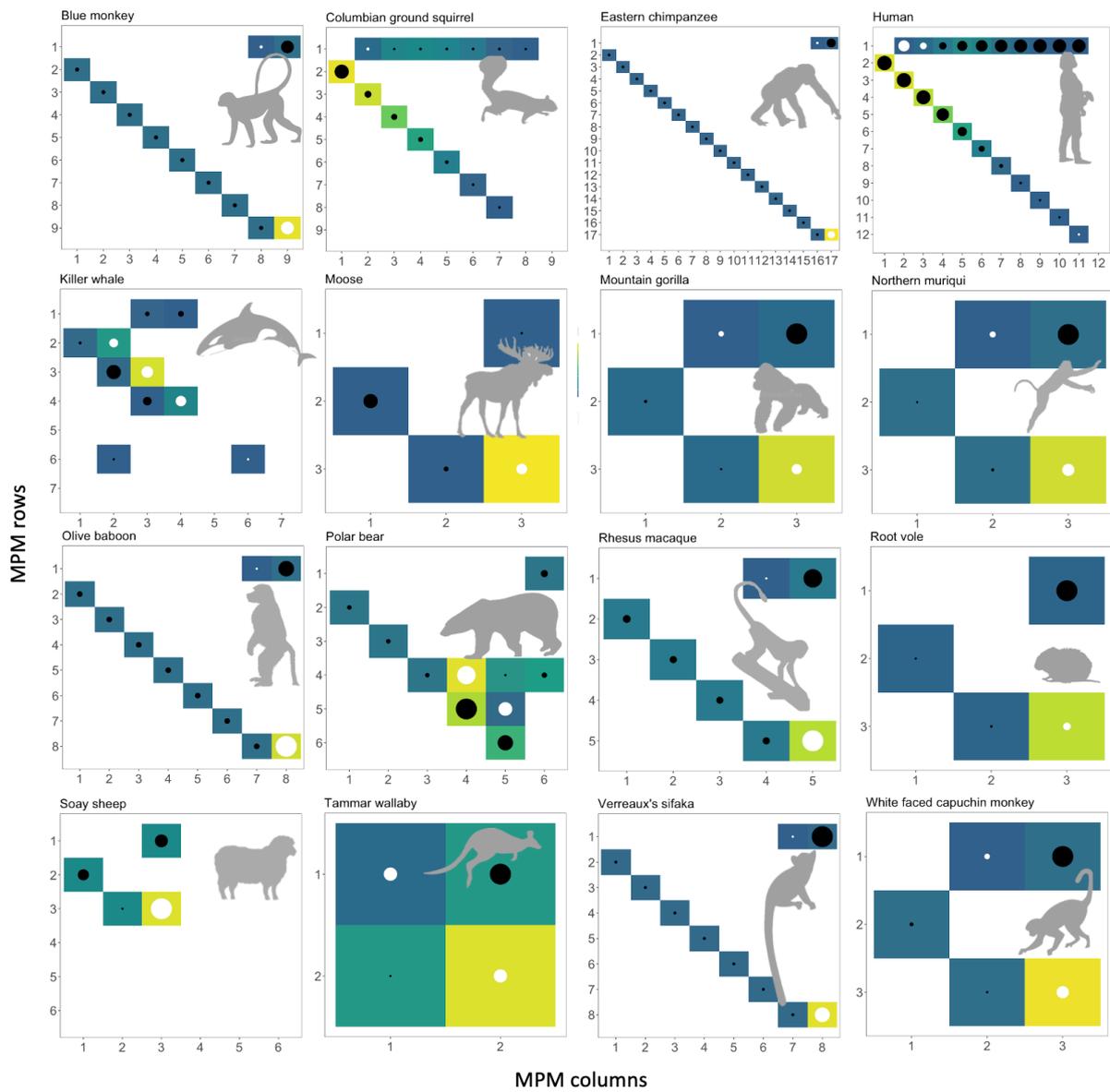
633 **Figure 2**



634

635

636 **Figure 3**



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638

639

640 **Figure legends**

641

642 **Figure 1.** A three-step framework proposed to: Step 1 - allocate species and/or populations
643 on a variance continuum (plot A, dots representing 50 hypothetical species). The variance
644 continuum operates at the between-populations level (see text) and is represented by
645 partitioning the sum of all the stochastic elasticities ($\Sigma E_{a_{ij}}^S$) into two compounds: i) sums of
646 stochastic elasticities with respect to the variance ($\Sigma E_{a_{ij}}^{S\sigma}$), and ii) sums of stochastic
647 elasticities with respect to the mean ($\Sigma E_{a_{ij}}^{S\mu}$). The first step of our framework shows the
648 variance compound of the sums of stochastic elasticities forming a continuum where the
649 right-hand side of the plot represents species (or populations) where a perturbation of
650 variance in demographic processes results in weak or no impact on λ_s (yellow dots). The
651 yellow-dotted species (or populations) can be classified as having potentially *buffered life-*
652 *cycles* – based on all the demographic processes. The left-hand side of the graph represents
653 species (or populations) where a perturbation of the variance in demographic processes
654 results in strong impact on λ_s (blue dots). Thus, the blue-dotted species (or populations) can
655 be classified as having potentially *unbuffered life cycles* – based on all the demographic
656 processes. The vertical axis delineates the values of the density distribution function,
657 indicating the number of species/populations at each value of $\Sigma E_{a_{ij}}^{S\sigma}$. The placement of data
658 points (species/populations) along the horizontal axis corresponds to their calculated values
659 of $\Sigma E_{a_{ij}}^{S\sigma}$ and is arranged linearly, while the breadth along the y-axis is solely for improved
660 visual comprehension. Step 2 - Access the linear selection pressures for individual species or
661 populations at within-species level (see text) (plot B). Step 2 displays the elasticities of the
662 deterministic population growth rate (λ_t) for a hypothetical population of wolf and reveals the
663 linear selection gradients, and which demographic processes are the most influential for λ_t .
664 Step 3 - Access the nonlinear selection pressures at the within-species level (see text) (plot

665 C). In the third step self-second derivatives for the corresponding demographic processes
666 from step 2 are displayed.

667

668 **Figure 2.** Results for step 1 of our framework showing the sum of stochastic elasticities with
669 respect to the variance $\Sigma E_{a_{ij}}^{S\sigma}$. The closer the $\Sigma E_{a_{ij}}^{S\sigma}$ is to zero, the weaker the impact of
670 variation in demographic processes on λ_s . The 40 populations from 34 species of mammals
671 from the COMADRE database are ranked into the variance continuum from potentially
672 buffered (right-hand side) to less buffered (left-hand side), since any variation in
673 demographic processes would strongly impact λ_s . Colors represent different taxonomic orders
674 with Primates occupying the right-hand side. Silhouettes: a) *Brachyteles hypoxantus*, b)
675 *Gorilla beringhei*, c) *Cercopithecus mitis*, d) *Urocyon v. columbianus*, e) *Mustela erminea*, f)
676 *Erythrocebus patas*, g) *Lepus americanus*, h) *Rattus fuscipes*, i) *Ovis aries*, j) *Homo sapiens*,
677 k) *Macropus eugenii*, and l) *Felis catus*. The vertical axis delineates the values of the density
678 distribution function, indicating the number of species/populations at each value of $\Sigma E_{a_{ij}}^{S\sigma}$.
679 The placement of data points (species/populations) along the horizontal axis corresponds to
680 their calculated values of $\Sigma E_{a_{ij}}^{S\sigma}$ and is arranged linearly, while the breadth along the y-axis is
681 solely for improved visual comprehension.

682

683 **Figure 3:** Results from steps 2 and 3 of the proposed framework (see Fig. 2B, C). The 16
684 plots represent populations where the MPMs built by ages were available in the COMADRE
685 database (see text). The color scale represents elasticity values for each of the demographic
686 processes in the MPM, where yellow represents high and blue low elasticity values. No color
687 means elasticity=0. Because the aim of step 2 is to identify the most impacting demographic
688 process within each species' life cycle (the within-populations level, see text) - not to

689 compare the elasticity values among species - each plot has its own scale (see end of legend).
690 The black dots represent negative self-second derivatives of λ_t - thus concave selection - and
691 the white dots represent positive self-second derivatives of λ_t - thus convex selection. The dot
692 sizes are scaled by the absolute value of self-second derivatives, where the smaller the dot,
693 the closer a self-second derivative is to 0, indicating weak or no nonlinearity. Large dots
694 indicate strong nonlinear selection forces. Scales ($E_{\min-\max}$ =elasticity minimum and maximum
695 value, $SSD_{\min-\max}$ =self-second derivative minimum and maximum value): Blue monkey $E_{\min-$
696 $\max}=0.00-0.52$, $SSD_{\min-\max}=-1.25-1.27$; Columbian ground squirrel: $E_{\min-\max}=0.00-0.23$,
697 $SSD_{\min-\max}=-1.48-0.01$; Eastern chimpanzee: $E_{\min-\max}=0.00-0.60$, $SSD_{\min-\max}=-4.39-2.59$;
698 Human: $E_{\min-\max}=0.00-0.18$, $SSD_{\min-\max}=-0.15-0.08$; Killer whale: $E_{\min-\max}=0.00-0.55$,
699 $SSD_{\min-\max}=-5.72-3.43$; Moose: $E_{\min-\max}=0.00-0.55$, $SSD_{\min-\max}=-0.66-0.36$; Mountain gorilla:
700 $E_{\min-\max}=0.00-0.81$, $SSD_{\min-\max}=-1.46-0.28$; Northern muriqui: $E_{\min-\max}=0.00-0.72$, $SSD_{\min-$
701 $\max}=-1.17-0.35$; Olive baboon: $E_{\min-\max}=0.00-0.54$, $SSD_{\min-\max}=-0.57-1.13$; Polar bear: $E_{\min-$
702 $\max}=0.00-0.26$, $SSD_{\min-\max}=-0.73-0.54$; Rhesus macaque: $E_{\min-\max}=0.00-0.51$, $SSD_{\min-\max}=-$
703 $0.54-0.71$; Root vole: $E_{\min-\max}=0.00-0.86$, $SSD_{\min-\max}=-2.54-0.22$; Soay sheep: $E_{\min-\max}=0.00-$
704 0.56 , $SSD_{\min-\max}=-0.22-0.40$; Tammar wallaby: $E_{\min-\max}=0.00-0.55$, $SSD_{\min-\max}=-0.64-0.34$;
705 White faced capuchin monkey: $E_{\min-\max}=0.00-0.66$, $SSD_{\min-\max}=-2.66-1.21$.

706

707 **Supplementary material – Data available in COMADRE Version 2.0.1 and results from**
708 **Step 1 of the framework**

709 **Table S1.** The metadata used in step 1 of our framework and the respective results presented
710 in the main text. The first four columns represent the information from where Matrix
711 Populations Models (MPMs) were extract precisely as presented in COMADRE 2.0.1.
712 Column titles differ from the database as “SpeciesAuthorComadre” is equivalent to
713 “SpeciesAuthor” and “SpeciesName” is equivalent to “SpeciesAccepted” in COMADRE
714 2.0.1. The remaining columns present the results of step 1, where we present the raw values

715 of $\Sigma E_{a_{ij}}^{S\mu}$ and $\Sigma E_{a_{ij}}^{S\sigma}$, their respective standard deviation, the stochastic population growth rate
716 λ_s , and the number of available matrices (# matrices). For ByAge, “TRUE” was assigned for
717 MPMs built by age or “FALSE” if otherwise.

SpeciesAuthorComadre	SpeciesName	CommonName	Order	ΣE
Homo_sapiens_subsp._sapiens	<i>Homo sapiens sapiens</i>	Human	Primates	1.003
Alces_alces	<i>Alces alces</i>	Moose	Artiodactyla	1.001
Antechinus_agilis	<i>Antechinus agilis</i>	Agile antechinus	Dasyuromorphia	1.111
Brachyteles_hypoxanthus	<i>Brachyteles hypoxanthus</i>	Northern muriqui	Primates	1.000
Callospermophilus_lateralis	<i>Callospermophilus lateralis</i>	Golden-mantled ground squirrel	Rodentia	1.054
Cebus_capucinus	<i>Cebus capucinus</i>	White faced capuchin monkey	Primates	1.000
Cercopithecus_mitis	<i>Cercopithecus mitis</i>	Blue monkey	Primates	1.000
Eumetopias_jubatus	<i>Eumetopias jubatus</i>	Northern sea lion; Steller sea lion	Carnivora	1.005
Felis_catus	<i>Felis catus</i>	Feral cat	Carnivora	1.136
Gorilla_beringei	<i>Gorilla beringei</i>	Mountain gorilla	Primates	1.000
Hippocamelus_bisulcus	<i>Hippocamelus bisulcus</i>	Huemul deer	Artiodactyla	1.002
Lepus_americanus	<i>Lepus americanus</i>	Snowshoe hare	Lagomorpha	1.294
Lycaon_pictus	<i>Lycaon pictus</i>	African wild dog	Carnivora	1.100
Macaca_mulatta_3	<i>Macaca mulatta</i>	Rhesus macaque	Primates	1.000
Macropus_eugenii	<i>Macropus eugenii</i>	Tammar wallaby	Diprotodontia	1.013
Marmota_flaviventris_2	<i>Marmota flaviventris</i>	Yellow-bellied marmot	Rodentia	1.007
Marmota_flaviventris_3	<i>Marmota flaviventris</i>	Yellow-bellied marmot	Rodentia	1.008
Microtus_oeconomus	<i>Microtus oeconomus</i>	Root vole	Rodentia	1.000
Mustela_erminea	<i>Mustela erminea</i>	Stoat	Carnivora	1.334
Orcinus_orca_2	<i>Orcinus orca</i>	Killer whale	Cetacea	1.001
Ovis_aries_2	<i>Ovis aries</i>	Soay sheep	Artiodactyla	1.033
Pan_troglodytes_subsp._schweinfurthii	<i>Pan troglodytes</i>	Eastern chimpanzee	Primates	1.000
Papio_cynocephalus	<i>Papio cynocephalus</i>	Olive baboon	Primates	1.000
Peromyscus_maniculatus_2	<i>Peromyscus maniculatus</i>	Deer mouse	Rodentia	1.010
Phocarctos_hookeri	<i>Phocarctos hookeri</i>	New Zealand sea lion	Carnivora	1.005
Propithecus_verreauxi	<i>Propithecus verreauxi</i>	Verreaux's sifaka	Primates	1.000

Puma_concolor_8	<i>Puma concolor</i>	Cougar	Carnivora	NA
Rattus_fuscipes	<i>Rattus fuscipes</i>	Bush rat	Rodentia	1.246
Spermophilus_armatus	<i>Urocitellus armatus</i>	Uinta ground squirrel	Rodentia	1.016
Spermophilus_armatus_2	<i>Urocitellus armatus</i>	Uinta ground squirrel	Rodentia	1.017
Spermophilus_columbianus	<i>Urocitellus columbianus</i>	Columbian ground squirrel	Rodentia	1.036
Spermophilus_columbianus_3	<i>Urocitellus columbianus</i>	Columbian ground squirrel	Rodentia	1.003
Ursus_americanus_subsp._floridanus	<i>Ursus americanus</i>	Florida black bear	Carnivora	1.003
Ursus_arctos_subsp._horribilis_5	<i>Ursus arctos</i>	Grizzly bear	Carnivora	1.001
Ursus_maritimus_2	<i>Ursus maritimus</i>	Polar bear	Carnivora	1.019
Brachyteles_hypoxanthus_2	<i>Brachyteles hypoxanthus</i>	Northern muriqui	Primates	1.000
Cebus_capucinus_2	<i>Cebus capucinus</i>	WhiteNAfaced capuchin monkey	Primates	1.000
Chlorocebus_aethiops_2	<i>Chlorocebus aethiops</i>	Vervet	Primates	1.075
Erythrocebus_patas	<i>Erythrocebus patas</i>	Patas monkey	Primates	1.051
Gorilla_beringei_subsp._beringei	<i>Gorilla beringei</i>	Mountain gorilla	Primates	1.000

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1 **A unified framework to quantify demographic buffering in natural populations**

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5 Gabriel Silva Santos^{1,2*}, Samuel J L Gascoigne^{3*}, André Tavares Corrêa Dias⁴, Maja Kajin
6 ^{3,5**♦}, Roberto Salguero-Gómez^{3♦}

7
8 1 National Institute of the Atlantic Forest (INMA), 29650-000, Santa Teresa, Espírito Santo,
9 Brazil. ssantos.gabriel@gmail.com

10 2 Department of Ecology, Graduate Program in Ecology and Evolution, Rio de Janeiro
11 State University, 524 São Francisco Xavier Street, 20550-900, Maracanã, Rio de Janeiro,
12 Brazil

13 3 Department of Biology, University of Oxford, South Parks Road, OX1 3RB, Oxford, UK.
14 samuel.gascoigne@pmb.ox.ac.uk, rob.salguero@biology.ox.ac.uk,
15 maja.kajin@biology.ox.ac.uk

16 4 Department of Ecology, Institute of Biology, Universidade Federal do Rio de Janeiro,
17 Avenida Carlos Chagas Filho 373, 21941-590 Rio de Janeiro, RJ, Brazil. atcdias@gmail.com

18 5 Department of Biology, Biotechnical Faculty, University of Ljubljana, Večna pot 111, 1000
19 Ljubljana, Slovenia

20
21 *Shared first authorship

22 **Corresponding author

23 ♦Shared senior authorship

24
25 AUTHOR CONTRIBUTIONS: GSS developed the initial concept, performed the statistical
26 analyses, and contributed to the first draft of the manuscript. SJLG developed the initial
27 concept, contributed to the first draft and all other versions of the manuscript, and generated
28 final figures. ATCD co-advised the project and contributed significantly to final versions of
29 the manuscript. MK developed and managed the project, contributed to the first draft and all
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50 **Abstract** (143/150 words)

51 The Demographic Buffering Hypothesis (DBH) predicts that natural selection reduces the
52 temporal fluctuations in demographic processes (such as survival, development, and
53 reproduction), due to their negative impacts on population dynamics. However, a
54 comprehensive approach that allows for the examination of demographic buffering patterns
55 across multiple species is still lacking. Here, we propose a three-step framework aimed at
56 quantifying demographic buffering. Firstly, we categorize species along a continuum of
57 variance based on the sums of stochastic elasticities. Secondly, we examine the linear
58 selection gradients, followed by the examination of nonlinear selection gradients as the third
59 step. With these three steps, our framework overcomes existing limitations of conventional
60 approaches to quantify demographic buffering, allows for multi-species comparisons, and
61 offers insight into the evolutionary forces that shape demographic buffering. We apply this
62 framework to mammal species and discuss both the advantages and potential of our
63 framework.

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67 Environmental stochasticity plays a pivotal role in shaping organisms' life histories (Bonsall
68 & Klug 2011). Nonetheless, how organisms will cope with the increasing variation in
69 environmental conditions expected under climate change (Boyce *et al.* 2006; Morris *et al.*
70 2008) is one of the most intriguing questions of ecology and evolution (Sutherland *et al.*
71 2013). Evolutionary demography offers a wide array of explanations for the evolutionary
72 processes that shape the diversity of demographic responses to environmental stochasticity
73 (Charlesworth 1994; Healy *et al.* 2019; Hilde *et al.* 2020; Pfister 1998; Tuljapurkar *et al.*
74 2009). The Demographic Buffering Hypothesis (*DBH*, hereafter) (Morris & Doak 2004;
75 Pélabon *et al.* 2020) is based on the fact that long-term stochastic population growth rate can
76 be expressed in terms of the geometric mean of the annual population growth rates
77 (Tuljapurkar 1982). As the geometric mean of λ increases, so does the long-term stochastic
78 population growth rate (λ_s , hereafter). However, increases in variance of λ decrease λ_s
79 (Morris & Doak 2004; Tuljapurkar 1982), and thus population persistence. This theoretical
80 context sets the stage for the DBH. The DBH predicts that life histories are under selection
81 pressure to minimise the negative impacts of environmental variation by constraining the
82 temporal variance of those demographic processes (*e.g.*, survival, development, reproduction)
83 to which population growth rate (*i.e.*, fitness) is most sensitive to (Gaillard & Yoccoz 2003;
84 Pfister 1998). The demographic pattern operating the DBH, *i.e.*, demographic buffering,
85 describes the selection-driven constraint on the temporal variance of the most impacting
86 demographic processes for the population growth rate (Hilde *et al.* 2020; Morris & Doak
87 2004; Pfister 1998). Here, we focus on the latter - on the emerging pattern of demographic
88 buffering in different animal life histories – rather than on the DBH itself.

89 A unified approach to unambiguously quantify demographic buffering is still missing.
90 Indeed, identifying demographic buffering remains challenging (Doak *et al.* 2005; Morris &
91 Doak 2004) for at least three reasons. First is the different interpretation of results from

92 correlational analyses (e.g., as in Pfister, 1998). Some authors have used the correlation
93 coefficient as an index to order species' life histories in a continuum ranging from buffered
94 (Spearman's correlation $\rho = <0$ between the sensitivity of λ to demographic processes and
95 their temporal variance) to labile ($\rho = >0$), regardless of the fit of the linear regression to
96 more or less scattered data (McDonald *et al.* 2017). In contrast, other researchers interpret the
97 absence of statistical support for demographic buffering as an alternative strategy where
98 variance in demographic process(es) is favoured to track environmental conditions (the so-
99 called Demographic Lability Hypothesis, *DLH* (e.g., Koons *et al.* 2009; Reed & Slade 2012;
100 Jäkäläniemi *et al.* 2013; Hilde *et al.* 2020). However, the increased temporal variance is a
101 necessary but not sufficient condition to constitute demographic lability – the increased
102 temporal variance needs to lead to (often high) change in the demographic process mean
103 value (Le Coeur *et al.* 2022).

104 The second obstacle to obtain generalisation across species' populations regarding
105 demographic buffering is the hierarchical level at which this phenomenon is typically
106 examined. Some studies base their investigations of demographic buffering on a
107 characteristic drawn from *the entire population model (between-populations level, hereafter)*
108 (McDonald *et al.* 2017; Reed & Slade 2012). At the between-populations level, a life history
109 is referred to as demographically buffered if the most important demographic process(es)
110 has(ve) low temporal variance (Le Coeur *et al.* 2022; Hilde *et al.* 2020; Morris & Doak 2004;
111 Pfister 1998). However, to understand how, why, and where demographic buffering occurs –
112 or not– and how buffering patterns might be modified in response to the environment, it is
113 essential to also consider the characteristics of the separate *components of population model*
114 (*within-populations level, hereafter*). Within a population, a given demographic process can
115 be buffered against while another can be labile to the environment (Barraquand & Yoccoz
116 2013; Jongejans *et al.* 2010; Koons *et al.* 2009). Thus far, studies have focused on either one

117 of the hierarchical levels, however, for a mechanistic understanding of how environmental
118 stochasticity shapes life histories, both between- and within-population levels need to be
119 addressed at the same time.

120 The third reason limiting a holistic understanding of demographic strategies in
121 stochastic environments are the challenges inherent to examining their underlying
122 mechanisms. Evidence for demographic buffering exists across some long-lived organisms
123 with complex life cycles, (Doak *et al.* 2005; Gaillard & Yoccoz 2003; McDonald *et al.* 2017;
124 Pfister 1998; Rotella *et al.* 2012), but also in short-lived species (Ferreira *et al.* 2013; Pfister
125 1998; Reed & Slade 2012). Importantly, these patterns of variation do not inform entirely on
126 how the life histories were shaped by natural selection. The beforementioned patterns of
127 variation are represented by *first-order* effects that perturbations in demographic processes
128 cause on the population growth rate (*i.e.*, elasticities). A first order effect informs us
129 regarding the population growth rate's sensitivity to *variation in demographic processes*.
130 While a second-order effect of perturbations in demographic processes reveals the population
131 growth rate's sensitivity to *autocorrelation* (Tuljapurkar 1990). Given so, integrating both,
132 first and second-order effects of perturbations in demographic processes on the population
133 growth rate, allows us to understand the behaviour of the fitness function at the vicinity of the
134 local maxima and/or minima.

135 When the relationship between fitness and a demographic process is linear, the
136 second-order derivatives of population growth rate with respect to demographic processes
137 equal zero. In such cases, natural selection acts on the mean value of a demographic process
138 (Shyu & Caswell 2014). However, nonzero second derivatives indicate a nonlinear
139 relationship between fitness and a demographic process (either concave if <0 , or convex if
140 >0) and thus provide additional and often overlooked characteristics of selection acting on

141 demographic processes – not only their mean values, but also their variances and covariances
142 (Brodie *et al.* 1995; Carslake *et al.* 2008; Shyu & Caswell 2014).

143 The sign (*i.e.*, >0 , $=0$, <0) of the self-second derivative of λ with respect to
144 demographic processes determines the type of (non)linear selection acting on a demographic
145 process. For instance, a negative self-second derivative for a given demographic process
146 describes a concave form of selection, commonly referred to as the \cap -shaped selection
147 (Caswell 1996, 2001; Shyu & Caswell 2014). This form of selection reduces the temporal
148 variance in said demographic process, thereby providing evidence of demographic buffering.
149 Conversely, a demographic process yielding a positive self-second derivative identifies a
150 convex, or U-shaped selection (Caswell 1996, 2001; Shyu & Caswell 2014). Such a selection
151 mechanism acts upon demographic processes amplifying their temporal variance, thus
152 potentially evidencing demographic lability (Le Coeur *et al.* 2022; Koons *et al.* 2009). The
153 evidence of lability is only potential, because to constitute demographic lability, the increased
154 variance needs to shift the mean value of a demographic process. The shift in the mean value
155 of a demographic process needs to overweight the negative effect of variance on the
156 population growth rate (Le Coeur *et al.* 2022).

157 The rich variation in demographic strategies across the Tree of Life is a result of
158 evolutionary processes that have shaped variance in demographic processes through time. In
159 this context, setting demographic buffering into the adaptive landscape context of linear and
160 nonlinear selection enables us to identify and quantify the evolutionary processes that
161 generate said demographic patterns. In this way, one will better understand how increased
162 variability of environmental conditions might act on the existing –and shape novel–
163 demographic strategies. However, we still lack a unified approach to constitute the signatures
164 of demographic buffering.

165 Here, we present a framework that quantifies demographic buffering. Our framework
166 provides a rich insight into the patterns of temporal variance in demographic processes
167 affected by environmental stochasticity. This framework involves categorizing species or
168 populations along a variance continuum based on the extent to which key demographic
169 processes are buffered by natural selection, thereby limiting their temporal variability. The
170 framework consists of four steps with a mix of well-known methods applied to stage-
171 structured demographic information (*e.g.*, matrix population models [Caswell 2001]; integral
172 projection models [Easterling et al. 2000]). First, we position species or populations on the
173 aforementioned continuum to assess the cumulative effect of the variance in their key
174 demographic processes on population growth rate at the between-populations level (see
175 below). Second, we investigate the presence of linear selection forces operating within the
176 life cycle of each species or population at the within-populations level (below). Third, we
177 explore the impact of non-linear selection forces acting within the life cycle of each species
178 or population, also at the within-populations level. The combination of these three steps
179 provides quantitative evidence for the occurrence of demographic buffering. Step four
180 suggests the further necessary analyses to identify demographic lability.

181 To demonstrate the applicability of our framework, we apply it to 40 populations of
182 34 mammal species sourced from the COMADRE database (Salguero-Gómez *et al.* 2016).
183 We showcase how the framework can provide valuable insights into the patterns of
184 demographic buffering across species. The framework offers novel, detailed insights into the
185 selection pressures that act *within* species' life cycles, thus allowing for a thorough
186 understanding of the evolutionary selection forces that shape the patterns of demographic
187 buffering across species. Beyond providing a quantitative, systematic toolset to quantify
188 buffering through three steps, we have also offer an alternative fourth step that briefly
189 outlines how to evidence lability.

190

191 **A unified framework to assess evidence of demographic buffering**

192 The evidence for demographic buffering has been mainly assessed using Matrix
193 Population Models (MPM; Pfister 1998; Rotella et al. 2012)). However, Integral Projection
194 Models (IPM; Rodríguez-Caro et al. 2020; Wang et al. 2023) can be equally applied for
195 identifying the demographic buffering signatures. Both MPMs and IPMs are stage-structured,
196 discrete-time demographic models (Caswell 2001; Ellner *et al.* 2016). For simplicity, here we
197 focus on MPMs, but note that the same approaches are as equally applicable to IPMs (Doak
198 *et al.* 2021; Griffith 2017). Throughout this manuscript, we refer to demographic processes as
199 both matrix entries a_{ij} (*i.e.*, upper-level parameters) and the vital rates that underline the
200 matrix elements (*i.e.*, lower-level parameters), and note that their conversion is
201 straightforward and described elsewhere (Franco & Silvertown 2004). The framework
202 operates on three steps.

203 The first step of our framework involves acquiring the relative impact of variation in
204 demographic processes on the stochastic growth rate, λ_s , the so-called stochastic elasticities,
205 E_{ij}^S (Haridas & Tuljapurkar 2005) (Figure 1A). The sum of all stochastic elasticities ($\Sigma E_{a_{ij}}^S$),
206 can be separated into two components to assess how temporal variance and mean values of
207 each demographic process impact λ_s . The first component represents the *sum of stochastic*
208 *elasticity of λ_s with respect to the variance* $\Sigma E_{a_{ij}}^{S\sigma}$, and the second represents the *sum of*
209 *stochastic elasticity of λ_s with respect to the mean* $\Sigma E_{a_{ij}}^{S\mu}$, where $\Sigma E_{a_{ij}}^S = \Sigma E_{a_{ij}}^{S\sigma} + \Sigma E_{a_{ij}}^{S\mu}$
210 (Haridas & Tuljapurkar 2005). Thus, the summation $\Sigma E_{a_{ij}}^{S\sigma}$ quantifies the summed effect to
211 which the stochastic population growth rate (λ_s) is influenced by changes in the variances of
212 the demographic processes within the population matrix.

213 A higher sum of stochastic elasticity of λ_s with respect to the variance of demographic
214 processes (*i.e.*, higher absolute value; $|\Sigma E_{a_{ij}}^{S\sigma}|$) indicates that small changes in the variance of
215 demographic processes would have a substantial impact on λ_s . In other words, the variance of
216 that demographic process is not constrained by selection, indicating absence of demographic
217 buffering. On the other hand, a lower (absolute) stochastic elasticity of λ_s with respect to the
218 variance of a given demographic process suggests that λ_s is less sensitive to such
219 perturbations, or, that variance of such demographic process is being constrained by natural
220 selection, thus pointing to demographic buffering (Haridas & Tuljapurkar 2005; Tuljapurkar
221 *et al.* 2003) (Fig. 1A).

222 The first step of the framework thus features the between-populations level and places
223 species or populations alongside a continuum. Species exhibiting unconstrained variance in
224 demographic processes (*i.e.*, possibly not buffered, Fig. 1A, blue dots) are positioned on the
225 left-hand side of the continuum. In contrast, species with constrained variance in
226 demographic processes (*i.e.*, possibly buffered, Fig. 1A, yellow dots) are positioned on the
227 right-hand side of the continuum. However, the left-hand side of the continuum does not
228 necessarily imply evidence of demographic lability. This is so because demographic lability
229 is defined as an increase in the *mean value* of a demographic process in response to improved
230 environmental conditions (Le Coeur *et al.* 2022). By examining $\Sigma E_{a_{ij}}^{S\sigma}$, we can visualize an
231 increase or decrease of the contribution that *variance* of demographic processes has on the
232 long-term population growth rate, while the mean value of a demographic process does not
233 change.

234 Step 1 of our framework examines the impacts that environmental variation has on the
235 long-term population growth rate, λ_s (Tuljapurkar *et al.* 2003). This means that the resulting
236 variance continuum in this step of the framework is based on how λ_s was affected by
237 variation in the key demographic parameter across all contiguous time periods. However,

238 Haridas & Tuljapurkar (2005) explicitly acknowledge that covariances between demographic
239 processes and serial correlations need to be investigated to diagnose buffering entirely. Our
240 approach does not use covariances neither serial correlation, but rather focuses on the second
241 derivatives of the population growth rate with respect to demographic processes and
242 elucidates how selection is acting on variance (step 3, below).

243 Steps 2 and 3 of the framework are conducted at the within-populations level. Once
244 species or populations are positioned along the variance continuum regarding the summed
245 effect of variation on λ_s , (step 1), one needs to zoom into each life cycle separately, analysing
246 the selection pressures acting on each one of the demographic processes composing the life
247 cycle (*i.e.*, population model). In doing so, one can inspect the selection pressures that have
248 generated the patterns found in step 1. Step 2 (Fig. 1B) requires obtaining the partial
249 derivatives of the deterministic population growth rate, λ_t , relative to all matrix elements of
250 the MPM of interest (*i.e.*, elasticities of λ_t w.r.t each demographic process in the MPM). Step
251 2 therefore informs on the impact that each of the demographic processes has on λ_t

252 Finally, in step 3, one assesses the pattern of nonlinear selection by using the self-
253 second derivatives of λ_t with respect to each demographic process (Fig. 1C). This step reveals
254 the potential nonlinear selection pressures on each of the demographic processes within a life
255 cycle. This step is key to understanding the evolutionary processes (*i.e.*, types of nonlinear
256 selection) that the demographic processes are subjected to. Without understanding the
257 evolutionary processes operating on the demographic processes, the pattern observed in step
258 1 might be artefactual. (e.g., Lawler et al. 2009)

259 Steps 2 and 3 of the framework feature selection pressures that have been averaged
260 over the contiguous time periods. This means that the resulting patterns are based on how λ_t
261 (obtained from averaging all sequential MPMs across the duration of the study) would be
262 affected if a demographic process were perturbed. Therefore, steps 2 and 3 are based on a

263 different information than step 1 and can thus complete our understanding of the role of
264 selection pressures on shaping demographic patterns across multiple species.

265 Another important asset of step 3 above includes the notion that the relative
266 importance (elasticity) of demographic processes themselves changes with changing
267 environment (Stearns 1992). In other words, the extent to which λ_t is sensitive to
268 perturbations in a specific demographic process is *dynamic* (Kroon *et al.* 2000). Thus, the
269 self-second derivatives generate information on how the sensitivity (or elasticity) of λ_t might
270 change. If the sensitivity (or elasticity) of λ_t can change, then it is important to know which
271 demographic processes are most prone to trigger such a change. In the example of a
272 hypothetical wolf species (Fig. 1), this means that if the reproduction of the third age-class
273 individuals (matrix element $a_{1,3}$) decreased, the sensitivity of λ_t to $a_{1,3}$ would increase (square
274 with the largest black dot, Fig. 1C). Consequently, with increased environmental variability,
275 the key demographic process might change from remaining in the fourth age class (matrix
276 element $a_{4,4}$, Fig. 1B) to reproduction of the third age-class (matrix element $a_{1,3}$, Fig. 1C).

277 Combining the three steps of our framework allows for a quantitative identification of
278 buffering. Steps 2 and 3 offer key insights as to *why* a given species or population is placed
279 on either the buffered or the non-buffered end of the variance continuum. A clear and
280 unequivocal evidence for support towards buffering consists of: (1) a species or population
281 being positioned near the 0 end of the continuum (the right-hand side) in step 1; (2) this
282 species' or populations' life cycle having one or more demographic processes with highest
283 elasticity values in step 2; and (3) the same demographic process displaying the highest
284 elasticity in step 2 with negative self-second derivative values in step 3. In this sense, Figure
285 1B shows that, for the chosen population of a hypothetical wolf species, the most important
286 demographic process is remaining in the fourth stage (MPM element $a_{4,4}$), as this
287 demographic process results in highest elasticity value (Fig. 1B yellow square). However,

288 Fig. 1C reveals that $a_{4,4}$ is under little selection pressure for variance reduction. Thus, there is
289 no clear evidence of buffering from the third step of the framework (*i.e.*, no concave selection
290 forces). This way, the lack of concave selection forces on the key demographic process within
291 wolf's life cycle explains why this species is placed on the left-hand side of the variance
292 continuum (Fig. 1A).

293 Species placed on the non-buffered end of the continuum is a necessary but not
294 sufficient condition for evidence demographic lability. It is key highlighting here that
295 demographic buffering and lability do not represent two extremes of the same continuum.
296 The variance continuum allocates the species or populations from strongly buffered to non-
297 buffered, but to test the for lability, a further step is needed.

298 Although not our primary goal here, we briefly introduce said step 4. To establish
299 compelling evidence of lability, it is essential to fulfil several further criteria. First, sufficient
300 data across various environments (over time or space) are required to construct reaction
301 norms that depict how a demographic process responds to environmental changes (Morris et
302 al., 2008; Koons et al., 2009), which can be challenging in terms of sufficient and high-
303 quality demographic and environmental data. Second, non-linear relationships between
304 demographic processes and the environment must be established based on the demographic
305 process-environment reaction norms. Lastly, demographic processes where an increase in the
306 mean value has a stronger positive impact on population growth rate than the detrimental
307 effect of increased variance needs to be identified. The latter condition is only met when the
308 demographic process-environment reaction norm takes a convex shape (resembling a "U"
309 shape), as described by Koons et al. (2009) and Morris et al. (2008). However, a study by
310 Barraquand and Yoccoz (2013) reported diverging results in this regard. Importantly, we note
311 that more likely than previously thought (*e.g.*, Pfister 1998), species do not exist as purely
312 buffering or labile, but that within populations, some vital rates may be buffered, other labile,

313 and others insensitive to the environment (*e.g.*, (Doak *et al.* 2005). Deciphering generality in
314 this likely complex pattern should attract much research attention going forward, in our
315 opinion.

316

317 **Demographic buffering in mammals: a case study using the unified framework**

318 We demonstrate the performance of our framework using 44 MPMs from 34 mammal
319 species. Mammals are of special interest here for two reasons: (1) mammalian life histories
320 have been well studied (Bielby *et al.* 2007; Gillespie 1977; Jones 2011; Stearns 1983); and
321 (2) some of their populations have already been assessed in terms of buffering, particularly
322 for primates (Campos *et al.* 2017; Morris *et al.* 2008, 2011; Reed & Slade 2012; Rotella *et al.*
323 2012). Together, the well-studied life histories and previous information about the occurrence
324 of buffering in mammals provide the necessary information to make accurate predictions and
325 validate the performance of the proposed framework.

326 We used Matrix Population Models from 40 out of 139 studies with mammals
327 available in the COMADRE database v.3.0.0 (Salguero-Gómez *et al.* 2016). These 40
328 populations encompass 34 species from eight taxonomic orders. We included these MPMs in
329 our analyses because they provide values of demographic processes (a_{ij}) for three or more
330 contiguous time periods, thus allowing us to obtain the stochastic elasticity of each a_{ij} .
331 Although we are aware that not all possible temporal variation in demographic processes may
332 have been expressed within this period, we assumed three or more transitions are enough to
333 provide sufficient variation for population comparison. At least three contiguous time periods
334 - a common selection criteria in comparative studies of stochastic demography (Compagnoni
335 *et al.* 2023) - also allowed to test and showcase our framework. Fortunately, several long-
336 lived species, characterized by low variation in their demographic processes, were studied for
337 a long time (*e.g.*, some primates in our dataset have been studied for over 20 years – Morris
338 *et al.* 2011). We removed the populations where either only survival or only reproduction

339 rates were reported, because of the impossibility to calculate the stochastic growth rate. A
340 detailed description of the analysed data and their original sources are available in
341 supplementary material (Supplementary Material, Table S1).

342 *Homo sapiens* was included in our analyses because it is the only mammalian species
343 in which second-order derivatives have been applied (Caswell 1996). Therefore, *Homo*
344 *sapiens* provides an ideal basis for comparisons among species. The data for *Homo sapiens*
345 were gathered from 26 modern populations located in various cities, allowing us to construct
346 a spatiotemporal variance. It is important to note that in this case, we are not working with
347 true temporal variance but rather a variance that encompasses both spatial and temporal
348 aspects.

349 For steps 2 and 3 of our framework, we utilized a subset of 16 populations (including
350 *Homo sapiens*) whose population projection matrices (MPMs) were organized by age. We
351 specifically selected these populations because their life cycles can be summarized by two
352 main demographic processes: survival and contribution to recruitment of new individuals.
353 The contribution to recruitment can be interpreted as either the mean reproductive output for
354 each age class or an approximation thereof, depending on how the matrices are structured
355 (Ebert 1999). One advantage of using such matrices is that they encompass only two types of
356 demographic processes, namely survival and recruitment, eliminating the need to account for
357 multiple transitions between different life stages.

358 To perform the step 1 of our framework and obtain the $\Sigma E_{a_{ij}}^{S^{\sigma}}$ (and $\Sigma E_{a_{ij}}^{S^{\mu}}$), we followed
359 Tuljapurkar *et al.* (2003) and Haridas & Tuljapurkar (2005). To perform step 2 of our
360 framework, we calculated the deterministic elasticities of each demographic process extracted
361 using the *popbio* package. All analyses were performed using R version 3.5.1 (R Core team,
362 2018). Finally, to perform the step 3 of our framework the self-second derivatives were

363 adapted from *demogR* (Jones 2007) following (Caswell 1996) and applied for the mean
364 MPM.

365 *Results*

366 We ranked 40 populations from the 34 identified mammal species according to the
367 cumulative impact of variation in demographic processes on λ_s using the step 1 of our
368 framework (Fig. 2). Additional information (including standard deviations of the elasticity
369 estimates and number of matrices available) is provided in the supplementary material (Table
370 S1). Most of the analysed orders were placed on the low-variance end of the variance
371 continuum (Fig. 2). The smallest contributions of variation in demographic processes (*i.e.*,
372 maximum value of $\Sigma E_{a_{ij}}^{S\sigma}$, note that $\Sigma E_{a_{ij}}^{S\sigma}$ ranges from 0 to -1), suggesting more buffered
373 populations, were assigned to Primates: northern muriqui (*Brachyteles hypoxantus*, $\Sigma E_{a_{ij}}^{S\sigma} = -$
374 $0.09 \times 10^{-4} \pm 0.12 \times 10^{-4}$) (mean \pm standard deviation) (Fig. 2 silhouette a), mountain gorilla
375 (*Gorilla beringhei*, $\Sigma E_{a_{ij}}^{S\sigma} = -0.24 \times 10^{-4} \pm 0.08 \times 10^{-4}$) (Fig. 2 silhouette b), followed by the
376 blue monkey (*Cercopithecus mitis*, $\Sigma E_{a_{ij}}^{S\sigma} = -0.63 \times 10^{-4} \pm 0.06 \times 10^{-4}$) (Fig. 2 silhouette c).
377 The first non-primate species placed near the low-variance end of the continuum was the
378 Columbian ground squirrel (*Urocitellus columbianus*, Rodentia, $\Sigma E_{a_{ij}}^{S\sigma} = -0.003 \pm 0.002$) (Fig.
379 2 silhouette d). The species with the highest contribution of variation in demographic
380 processes placed at the high-variance end of the continuum was the stoat (*Mustela erminea*,
381 Carnivora, $\Sigma E_{a_{ij}}^{S\sigma} = -0.35 \pm 0.02$) (Fig. 2 silhouette e). All the 14 primate populations
382 displayed potential evidence of buffering, occupying the right-hand side of the variance
383 continuum, with the exception of the Patas monkey (*Erythrocebus patas*, Primates, $\Sigma E_{a_{ij}}^{S\sigma} = -$
384 0.05 ± 0.03) (Fig. 2 silhouette f). The snowshoe hare (*Lepus americanus*, Lagomorpha, $\Sigma E_{a_{ij}}^{S\sigma}$

385 = -0.29 ± 0.16) (Fig. 2 silhouette g) and the Bush rat (*Rattus fuscipes*, Rodentia, $\Sigma E_{a_{ij}}^{S\sigma} = -0.25$
386 ± 0.03) (Fig. 2 silhouette h) appear on the high-variance end of the continuum.

387 As predicted for the steps 2 and 3, we could not observe a clear pattern in support of
388 buffering. This finding means that the demographic processes with the highest elasticity
389 values failed to display strongly negative self-second derivatives (Fig. 3). Particularly for
390 majority of primates - with the lack or minor temporal variation in demographic processes -
391 demographic processes with high elasticities had positive values for the self-second
392 derivatives (indicated by yellow squares with white dots in Fig. 3). Examples of primate
393 species exhibiting high elasticities and positive values for the self-second derivatives and
394 include northern muriqui (*Brachyteles hypoxanthus*), mountain gorilla (*Gorilla beringei*),
395 white-faced capuchin monkey (*Cebus capucinus*), rhesus monkey (*Macaca mulatta*), blue
396 monkey (*Cercopithecus mitis*), Verreaux's sifaka (*Propithecus verreauxi*) and olive baboon
397 (*Papio cynocephalus*) (Fig. 3). This implies that the key demographic processes influencing
398 λ_t are not subject to selective pressure for reducing their temporal variability. However, even
399 though the primates were positioned closer to the low-variance end of the continuum in step
400 1, the evidence from steps 2 and 3 does not support the occurrence of buffering in the most
401 influential demographic processes.

402 The killer whale showed similar controversy between step 1 and steps 2-3 results as
403 most primates. In step 1, the killer whale was positioned at the buffered end of the variance
404 continuum (*Orcinus orca*, Cetacea, $\Sigma E_{a_{ij}}^{S\sigma} = -0.70 \times 10^{-4} \pm 1.04 \times 10^{-5}$) (Fig. 2 silhouette not
405 shown). However, steps 2 and 3 show that the three demographic processes in killer whale
406 life cycle with highest elasticity values (matrix elements $a_{2,2}$, $a_{3,3}$ and $a_{4,4}$) are not under
407 selection pressures for reducing their temporal variance, but the opposite (depicted by yellow
408 and green squares with white dots, Fig. 3).

409 The only primate species exhibiting evidence of buffering in steps 2 and 3 was
410 human. In human, demographic parameters representing survival from first to second age
411 class (matrix element $a_{2,1}$) displayed high elasticities and negative self-second derivatives
412 (depicted as yellow squares with black dots in Fig. 3). Evidence supporting buffering was
413 also found in the Columbian ground squirrel (*Urocitellus columbianus*), where, similar to
414 humans, survival from the first to the second age class (matrix element $a_{2,1}$) showed
415 indications of selection acting to reduce $a_{2,1}$ variance. Accordingly, the Columbian ground
416 squirrel was positioned close to the buffered end of the variance continuum in step 1. Hence,
417 the Columbian ground squirrel was the sole species with consistent evidence of buffering
418 across all three steps of the framework.

419 The Soay sheep (*Ovis aries*) was the species furthest from the buffered end of the
420 variance continuum that enabled to perform steps 2 and 3. For the Soay sheep, remaining in
421 the third age class (matrix element $a_{3,3}$) has the major influence on λ_t and is under selection
422 pressure to have its variance increased. The latter characteristics reveal potential conditions
423 for lability even though the species is placed closer to the buffered end of the variance
424 continuum.

425 Steps 2 and 3 illustrate the importance of examining buffering evidence on the within-
426 populations level. These two steps of the framework identify the simultaneous acting of
427 concave and convex selection on different demographic processes within a single life cycle.
428 In polar bear (*Ursus maritimus*), the key demographic process (matrix element $a_{4,4}$) is under
429 convex selection, as depicted by a yellow square with a white dot in Fig. 3. However, the
430 demographic process with the second highest elasticity value (matrix element $a_{5,4}$) is under
431 strong concave selection (depicted by a light green square with a black dot in Fig. 3).

432 By adding step 3 to the framework, another important information was accessed. The
433 high absolute values of self-second derivatives (large dots, either black or white, Fig. 3)
434 indicate where the sensitivity of λ_t to demographic parameters is itself prone to environmental
435 changes. For instance, if the value of $a_{5,4}$ for polar bear increased, the sensitivity of λ_t to $a_{5,4}$
436 would decrease because the self-second derivative of $a_{5,4}$ is highly negative (depicted by the
437 largest black dot in polar bear MPM). Vice versa holds for the $a_{4,4}$ demographic process,
438 where an increase in the value of $a_{4,4}$ would increase λ_t 's sensitivity to $a_{4,4}$, because the self-
439 second derivative of $a_{5,4}$ is highly positive (depicted by the largest white dot in polar bear
440 MPM). Thus, sensitivities (or equally elasticities) of demographic processes with high
441 absolute values for self-second derivatives can easily change..

442 **Discussion**

443 In the Anthropocene, identifying and quantifying mechanisms of species responses to
444 stochastic environments holds crucial importance. This importance is particularly tangible in
445 the context of the unprecedented environmental changes and uncertainties that impact the
446 dynamics and persistence of natural populations (Boyce *et al.* 2006). Correlational
447 demographic analysis, whereby the importance of demographic processes and their temporal
448 variability is examined (Pfister 1998), has attempted to identify how species may buffer
449 against the negative effects of environmental stochasticity. However, these widely used
450 approaches have important limitations (see Introduction and Hilde *et al.* 2020). One
451 significant limitation is the issue of measurement scale concerning demographic processes
452 (Hilde *et al.* 2020; Morris & Doak 2004). Demographic processes, such as birth rates, death
453 rates, immigration, and emigration, operate at various temporal and spatial scales. The choice
454 of scale at which these processes are measured can impact the outcomes of correlational
455 demographic analysis (Bjørkvoll *et al.* 2016). Our novel framework overcomes said

456 limitations by providing a rigorous approach to quantify demographic buffering (Hilde et al.
457 2020; Pfister 1998).

458 Evidencing demographic buffering is not straightforward. Indeed, through the
459 analysis of stochastic population growth rate (λ_s) in our application of the framework to 44
460 populations of 34 species, we identify the highest density of natural populations near the
461 buffered end of the variance continuum (step 1). However, we show that the same species
462 then fail to exhibit signs of concave (\cap -shaped) selection on the key demographic parameters
463 when further analyses are performed averaging the variation across the duration of each study
464 (steps 2 and 3). This finding confirms that placing the species near the buffered end of the
465 variance continuum is *necessary* but not *sufficient* to diagnose demographic buffering.
466 Indeed, buffering occurs when concave selection forces act on the key demographic
467 parameter (Caswell 1996, 2001; Shyu & Caswell 2014).

468 Combining the three steps into a unified framework is of utmost importance. In steps
469 2 and 3 of the framework, we find relatively limited overall evidence of buffering in the
470 examination of our 16 (out of 34 in step 1) studied animal species. Step 3 of our framework
471 reveals that the role of natural selection shaping temporal variation in demographic processes
472 is more complex than expected. Indeed, demographic processes within our study populations
473 are often under a mix of convex and concave selection. This mix of selection patterns was
474 already suggested by Doak *et al.* (2005). Here, only two out of 16 mammal species revealed
475 concave selection acting on the key demographic processes (Columbian ground squirrel
476 [*Uroditellus columbianus*], and humans, [*Homo sapiens sapiens*]). These two species were
477 also placed near the buffered end of the variance continuum, therefore meeting all the
478 necessary conditions to diagnose buffering. However, finding 12.5% (two out of 16) species
479 that meet the criteria for demographic buffering is not in concordance with previous studies.
480 Evidence of buffering has been reported across 22 ungulate species (Gaillard & Yoccoz

481 2003). In the one ungulate we examined, the moose (*Alces alces*), we find only partial
482 support for buffering in adult survival, since this species is placed near the buffered end of
483 the variance continuum in step 1 but does not show concave selection pressures on adult
484 survival in step 2/3, as would be necessary to confirm the occurrence of buffering.
485 It is worth noting that a varying number of matrices per species were employed, ranging from
486 1 to 21, with an average of 8.1 matrices per species (as shown in Table S1). Naturally, having
487 a greater number of matrices is preferred in such analyses. Furthermore, while the size of
488 matrices (matrix dimensions) does not directly bias the results of our framework in any way –
489 since steps 2 and 3 are shown for all the demographic processes independent of matrix
490 dimension – potential implications of varying matrix dimensions should be further
491 investigated in the future.

492 Our overall findings reveal varying levels of support for the notion that adult survival
493 in long-lived species tends to be buffered. Indeed, Gaillard *et al.* (1998) found that adult
494 female survival varied considerably less than juvenile survival in large herbivores. This
495 finding was also supported by further studies in ungulates and small rodents (Gaillard &
496 Yoccoz 2003), turtles (Heppell 1998), vertebrates and plants (Pfister 1998), and more
497 recently across nine (out of 73) species of plants (McDonald *et al.* 2017).

498 When placing our study species along a variance continuum (step 1), primates tend to
499 be located on the buffered end. However, most primates displayed convex –instead of the
500 expected concave– selection on adult survival. Similar results, where the key demographic
501 process failed to display constrained temporal variability, have been reported for long-lived
502 seabirds (Doherty *et al.* 2004). One explanation for the unexpected convex selection on adult
503 survival involves trade-offs, as suggested by (Doak *et al.* 2005). When two demographic
504 parameters are negatively correlated, the variance of population growth rate (λ) can be
505 increased or decreased (Compagnoni *et al.* 2016; Evans & Holsinger 2012). The well-

506 established trade-off between survival and fecundity (Roff & Fairbairn 2007; Stearns 1992)
507 might explain the observed deviation of our results. Because variation in primate recruitment
508 is already constrained by physiological limitations (Campos *et al.* 2017), when adult survival
509 and recruitment are engaged in a trade-off, this trade-off might lead to our unexpected result.
510 Correlations among demographic processes (positive and negative) inherently influence the
511 biological limits of variance (Haridas & Tuljapurkar, 2005). This is because the magnitude of
512 variation in a particular demographic process is constrained by (the variation of) other
513 demographic processes that exert an influence on it. Not surprisingly, correlations among
514 demographic processes have been shown to be strongly subjected to ecological factors (Fay
515 *et al.* 2022). Here, future studies may benefit from deeper insights via cross-second
516 derivatives (Caswell 1996, 2001) to investigate correlations among demographic processes.

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

525

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532

533 **Data availability**

534 The demographic data used in this paper are open-access and available in the COMADRE
535 Animal Matrix Database (<https://compadre-db.org/Data/Comadre>). A list of the studies and
536 species used here is available in Supplementary Material (Table S1). The data and code
537 supporting the results can be accessed here:
538 https://github.com/SamuelGascoigne/Demographic_buffering_unified_framework.

539

540 **References**

- 541 Barraquand, F. & Yoccoz, N.G. (2013). When can environmental variability benefit
542 population growth? Counterintuitive effects of nonlinearities in vital rates. *Theor Popul*
543 *Biol*, 89, 1–11.
- 544 Bielby, J., Mace, G.M., Bininda-Emonds, O.R.P., Cardillo, M., Gittleman, J.L., Jones, K.E.,
545 *et al.* (2007). The Fast-Slow Continuum in Mammalian Life History: An Empirical
546 Reevaluation. *Am Nat*, 169, 748–757.
- 547 Bjørkvoll, E., Lee, A.M., Grøtan, V., Saether, B.-E., Stien, A., Engen, S., *et al.* (2016).
548 Demographic buffering of life histories? Implications of the choice of measurement
549 scale. *Ecology*, 97, 40–47.
- 550 Bonsall, M.B. & Klug, H. (2011). The evolution of parental care in stochastic environments.
551 *J Evol Biol*, 24, 645–655.
- 552 Boyce, M.S., Haridas, C. V., Lee, C.T., Boggs, C.L., Bruna, E.M., Coulson, T., *et al.* (2006).
553 Demography in an increasingly variable world. *Trends Ecol Evol*, 21, 141–148.
- 554 Brodie, E.I., Moore, A. & Janzen, F. (1995). Visualizing and quantifying natural selection.
555 *Trends Ecol Evol*, 10, 313–318.
- 556 Campos, F.A., Morris, W.F., Alberts, S.C., Altmann, J., Brockman, D.K., Cords, M., *et al.*
557 (2017). Does climate variability influence the demography of wild primates? Evidence
558 from long-term life-history data in seven species. *Glob Chang Biol*, 23, 4907–4921.
- 559 Carlslake, D., Townley, S. & Hodgson, D.J. (2008). Nonlinearity in eigenvalue-perturbation
560 curves of simulated population projection matrices. *Theor Popul Biol*, 73, 498–505.
- 561 Caswell, H. (1996). Second Derivatives of Population Growth Rate: Calculation and
562 Applications. *Ecology*, 77, 870–879.

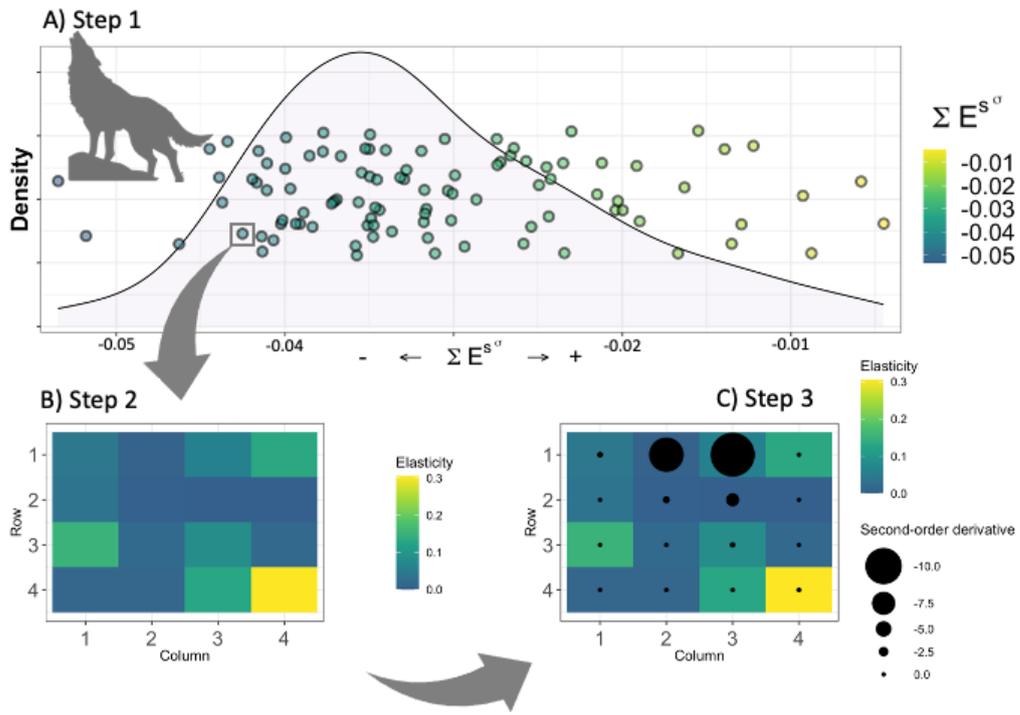
- 563 Caswell, H. (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*.
564 Sinauer Associates Inc. Publishers, Sunderland, Massachusetts, USA.
- 565 Charlesworth, B. (1994). *Evolution in age-structured populations*. second edi. Cambridge
566 University Press.
- 567 Le Coeur, C., Yoccoz, N.G., Salguero-Gómez, R. & Vindenes, Y. (2022). Life history
568 adaptations to fluctuating environments: Combined effects of demographic buffering
569 and lability. *Ecol Lett*, 1–13.
- 570 Compagnoni, A., Bibian, A.J., Ochocki, B.M., Rogers, H.S., Schultz, E.L., Sneek, M.E., *et*
571 *al.* (2016). The effect of demographic correlations on the stochastic population dynamics
572 of perennial plants. *Ecol Monogr*, 86, 480–494.
- 573 Compagnoni, A., Evers, S. & Knight, T. (2023). Spatial replication can best advance our
574 understanding of population responses to climate. *bioRxiv*,
575 <https://doi.org/10.1101/2022.06.24.497542>.
- 576 Doak, D.F., Morris, W.F., Pfister, C., Kendall, B.E. & Bruna, E.M. (2005). Correctly
577 Estimating How Environmental Stochasticity Influences Fitness and Population Growth.
578 *Am Nat*, 166, E14–E21.
- 579 Doak, D.F., Waddle, E., Langendorf, R.E., Louthan, A.M., Isabelle Chardon, N., Dibner,
580 R.R., *et al.* (2021). A critical comparison of integral projection and matrix projection
581 models for demographic analysis. *Ecol Monogr*, 91, e01447.
- 582 Doherty, P.F., Schreiber, E.A., Nichols, J.D., Hines, J.E., Link, W.A., Schenk, G.A., *et al.*
583 (2004). Testing life history predictions in a long-lived seabird: A population matrix
584 approach with improved parameter estimation. *Oikos*, 105, 606–618.
- 585 Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000). Size-Specific Sensitivity: Applying a
586 New Structured Population Model. *Ecology*, 81, 694–708.
- 587 Ellner, S.P., Childs, D.Z. & Rees, M. (2016). *Data-driven Modelling of Structured*
588 *Populations. A practical guide to the Integral Projection Model*. Lecture Notes on
589 Mathematical Modelling in the Life Sciences. Springer International Publishing, Cham.
- 590 Evans, M.E.K. & Holsinger, K.E. (2012). Estimating covariation between vital rates : A
591 simulation study of connected vs . separate generalized linear mixed models (GLMMs).
592 *Theor Popul Biol*, 82, 299–306.
- 593 Fay, R., Hamel, S., van de Pol, M., Gaillard, J.M., Yoccoz, N.G., Acker, P., *et al.* (2022).
594 Temporal correlations among demographic parameters are ubiquitous but highly
595 variable across species. *Ecol Lett*, 25, 1640–1654.
- 596 Ferreira, M., Kajin, M., Vieira, M., Zangrandi, P., Cerqueira, R. & Gentile, R. (2013). Life
597 history of a neotropical marsupial: Evaluating potential contributions of survival and
598 reproduction to population growth rate. *Mamm Biol*, 78, 406–411.
- 599 Franco, M. & Silvertown, J. (2004). A comparative demography of plants based upon
600 elasticities of vital rates. *Ecology*, 85, 531–538.

- 601 Gaillard, J.-M. & Yoccoz, N. (2003). Temporal Variation in Survival of Mammals: a Case of
602 Environmental Canalization? *Ecology*, 84, 3294–3306.
- 603 Gillespie, J.H. (1977). Natural Selection for Variances in Offspring Numbers: A New
604 Evolutionary Principle. *Am Nat*, 111, 1010–1014.
- 605 Griffith, A.B. (2017). Perturbation approaches for integral projection models. *Oikos*, 126,
606 1675–1686.
- 607 Haridas, C.V. & Tuljapurkar, S. (2005). Elasticities in Variable Environments: Properties and
608 Implications. *Am Nat*, 166, 481–495.
- 609 Healy, K., Ezard, T.H.G., Jones, O.R., Salguero-Gómez, R. & Buckley, Y.M. (2019). Animal
610 life history is shaped by the pace of life and the distribution of age-specific mortality and
611 reproduction. *Nat Ecol Evol*, 3, 1217–1224.
- 612 Heppell, S.S. (1998). Application of Life-History Theory and Population Model Analysis to
613 Turtle Conservation. *Copeia*, 1998, 367.
- 614 Hilde, C.H., Gamelon, M., Sæther, B.-E., Gaillard, J.-M., Yoccoz, N.G. & Pélabon, C.
615 (2020). The Demographic Buffering Hypothesis: Evidence and Challenges. *Trends Ecol*
616 *Evol*, 35, 523–538.
- 617 Jäkäläniemi, A., Ramula, S. & Tuomi, J. (2013). Variability of important vital rates
618 challenges the demographic buffering hypothesis. *Evol Ecol*, 27, 533–545.
- 619 Jones, J.H. (2007). demogR: A Package for the Construction and Analysis of Age-structured
620 Demographic Models in R. *J Stat Softw*, 22, 1–28.
- 621 Jones, J.H. (2011). Primates and the evolution of long, slow life histories. *Current Biology*,
622 21, R708–R717.
- 623 Jongejans, E., De Kroon, H., Tuljapurkar, S. & Shea, K. (2010). Plant populations track
624 rather than buffer climate fluctuations. *Ecol Lett*, 13, 736–743.
- 625 Koons, D.N., Pavard, S., Baudisch, A. & Jessica E. Metcalf, C. (2009). Is life-history
626 buffering or lability adaptive in stochastic environments? *Oikos*, 118, 972–980.
- 627 Kroon, H. de, van Groenendael, J. & Ehrlén, J. (2000). Elasticities: A review of methods and
628 model limitations.
- 629 McDonald, J.L., Franco, M., Townley, S., Ezard, T.H.G., Jelbert, K. & Hodgson, D.J. (2017).
630 Divergent demographic strategies of plants in variable environments. *Nat Ecol Evol*, 1,
631 0029.
- 632 Morris, W.F., Altmann, J., Brockman, D.K., Cords, M., Fedigan, L.M., Pusey, A.E., *et al.*
633 (2011). Low Demographic Variability in Wild Primate Populations: Fitness Impacts of
634 Variation, Covariation, and Serial Correlation in Vital Rates. *Am Nat*, 177, E14–E28.
- 635 Morris, W.F. & Doak, D.F. (2004). Buffering of Life Histories against Environmental
636 Stochasticity: Accounting for a Spurious Correlation between the Variabilities of Vital
637 Rates and Their Contributions to Fitness. *Am Nat*, 163, 579–590.

- 638 Morris, W.F., Pfister, C.A., Tuljapurkar, S., Haridas, C. V., Boggs, C.L., Boyce, M.S., *et al.*
639 (2008). Longevity can buffer plant and animal populations against changing climatic
640 variability. *Ecology*, 89, 19–25.
- 641 Pélabon, C., Hilde, C.H., Einum, S. & Gamelon, M. (2020). On the use of the coefficient of
642 variation to quantify and compare trait variation. *Evol Lett*, 4, 180–188.
- 643 Pfister, C. (1998). Patterns of variance in stage-structured populations: Evolutionary
644 predictions and ecological implications. *Proceedings of the National Academy of*
645 *Sciences*, 95, 213–218.
- 646 Reed, A.W. & Slade, N.A. (2012). Buffering and plasticity in vital rates of oldfield rodents.
647 *Journal of Animal Ecology*, 81, 953–959.
- 648 Rodríguez-Caro, R.C., Capdevila, P., Graciá, E., Barbosa, J.M., Giménez, A. & Salguero-
649 Gómez, R. (2020). The demographic buffering strategy has a threshold of effectiveness
650 to increases in environmental stochasticity. *bioRxiv*, 1–41.
- 651 Roff, D.A. & Fairbairn, D.J. (2007). The evolution of trade-offs: Where are we? *J Evol Biol*,
652 20, 433–447.
- 653 Rotella, J.J., Link, W.A., Chambert, T., Stauffer, G.E. & Garrott, R.A. (2012). Evaluating the
654 demographic buffering hypothesis with vital rates estimated for Weddell seals from 30
655 years of mark – recapture data, 162–173.
- 656 Salguero-Gómez, R., Jones, O.R., Archer, C.R., Bein, C., de Buhr, H., Farack, C., *et al.*
657 (2016). COMADRE: A global data base of animal demography. *Journal of Animal*
658 *Ecology*, 85, 371–384.
- 659 Shyu, E. & Caswell, H. (2014). Calculating second derivatives of population growth rates for
660 ecology and evolution. *Methods Ecol Evol*, 5, 473–482.
- 661 Stearns, S. (1992). *The Evolution of Life Histories*. Oxford University Press, New York,
662 USA.
- 663 Stearns, S.C. (1983). The Influence of Size and Phylogeny on Patterns of Covariation among
664 Life-History Traits in the Mammals. *Oikos*, 41, 173.
- 665 Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron,
666 D.D., *et al.* (2013). Identification of 100 fundamental ecological questions. *Journal of*
667 *Ecology*, 101, 58–67.
- 668 Tuljapurkar, S., Gaillard, J.-M. & Coulson, T. (2009). From stochastic environments to life
669 histories and back. *Philosophical Transactions of the Royal Society B: Biological*
670 *Sciences*, 364, 1499–1509.
- 671 Tuljapurkar, S., Horvitz, C.C. & Pascarella, J.B. (2003). The Many Growth Rates and
672 Elasticities of Populations in Random Environments. *Am Nat*, 162, 489–502.
- 673 Tuljapurkar, S.D. (1982). Population dynamics in variable environments. III. Evolutionary
674 dynamics of r-selection. *Theor Popul Biol*, 21, 141–165.

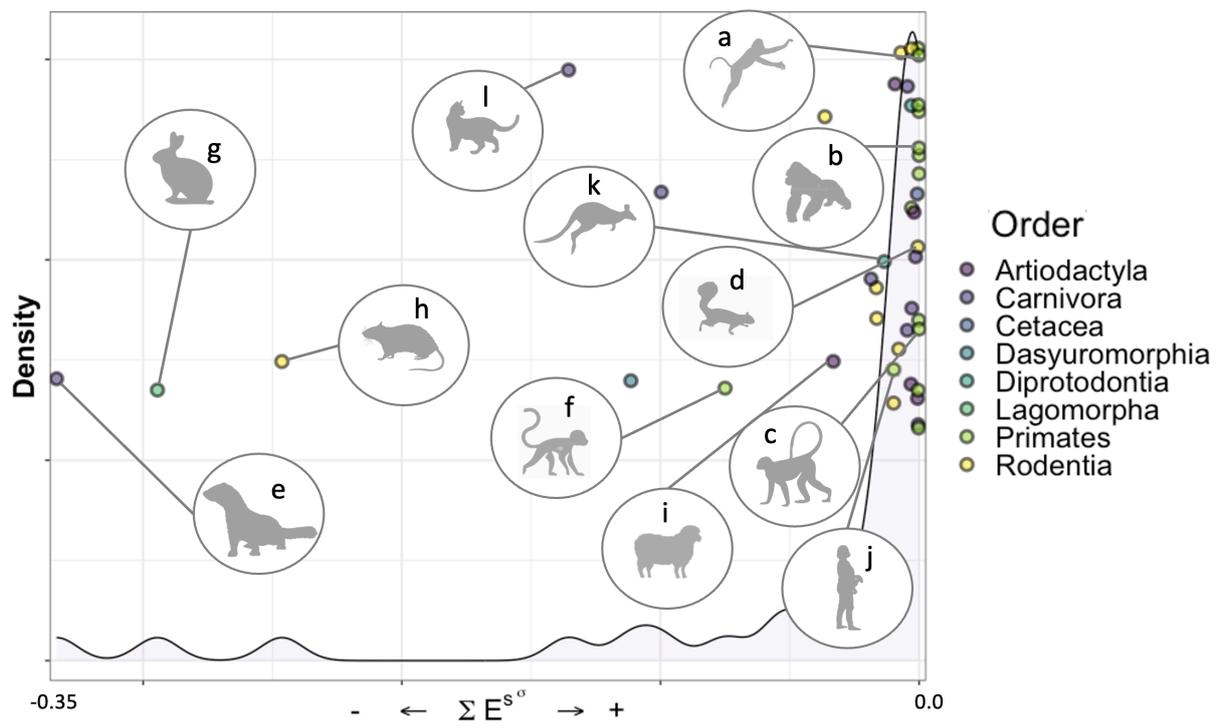
- 675 Tuljapurkar, S. (1990). Population Dynamics in Variable Environments. In: *Lecture notes in*
676 *Biomathematics*, Lecture Notes in Biomathematics (ed. Levin, S.). Springer Berlin
677 Heidelberg.
- 678 Vázquez, D.P., Gianoli, E., Morris, W.F. & Bozinovic, F. (2017). Ecological and
679 evolutionary impacts of changing climatic variability. *Biological Reviews*, 92, 22–42.
- 680 Wang, J., Yang, X., Silva Santos, G., Ning, H., Li, T., Zhao, W., *et al.* (2023). Flexible
681 demographic strategies promote the population persistence of a pioneer conifer tree
682 (*Pinus massoniana*) in ecological restoration. *For Ecol Manage*, 529, 120727.
- 683
- 684

685 **Figure 1**



686

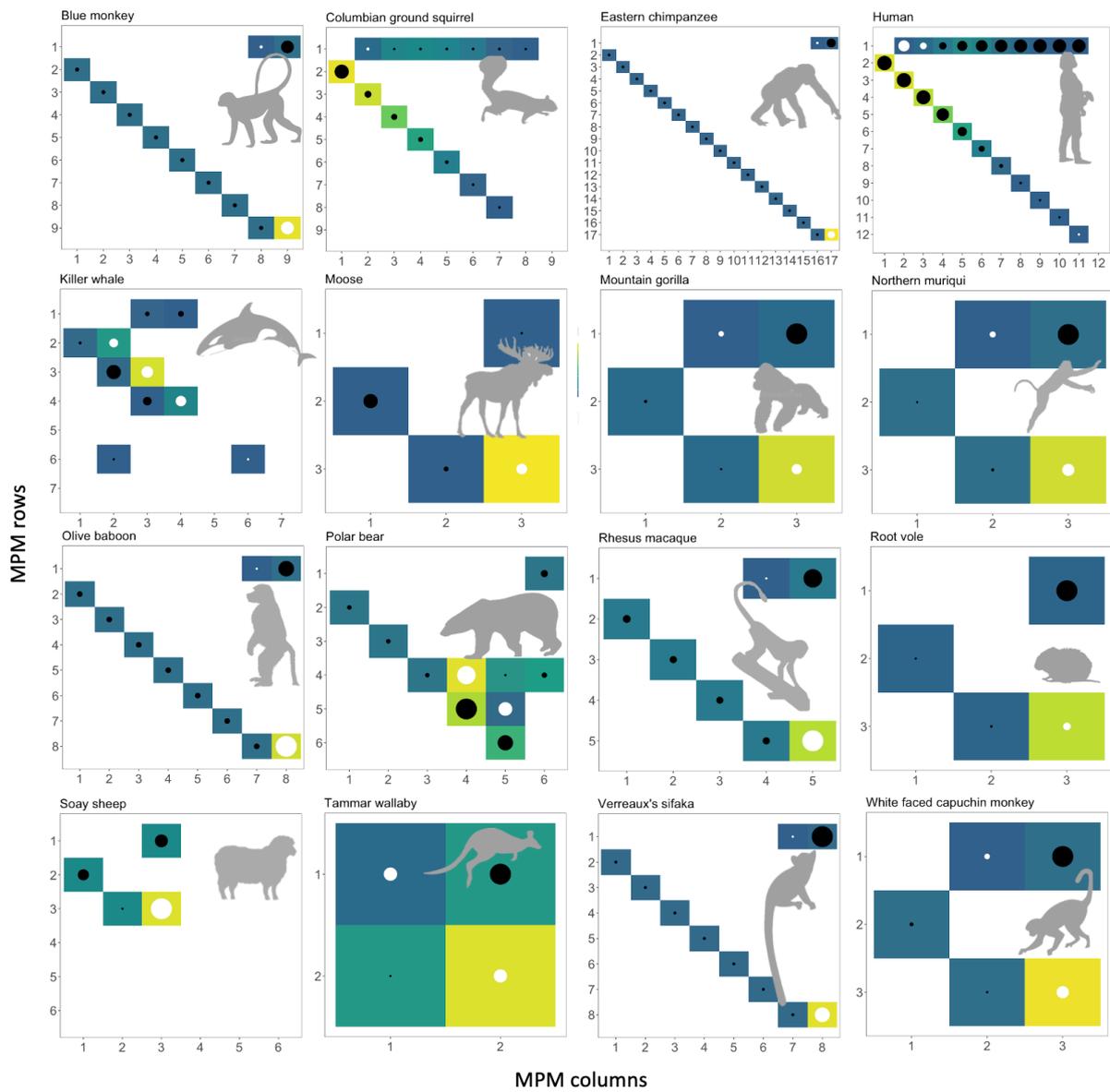
687 **Figure 2**



688

689

690 **Figure 3**



691

692

693

694 **Figure legends**

695

696 **Figure 1.** A three-step framework proposed to: Step 1 - allocate species and/or populations
697 on a variance continuum (plot A, dots representing 50 hypothetical species). The variance
698 continuum operates at the between-populations level (see text) and is represented by
699 partitioning the sum of all the stochastic elasticities ($\Sigma E_{a_{ij}}^S$) into two compounds: i) sums of
700 stochastic elasticities with respect to the variance ($\Sigma E_{a_{ij}}^{S\sigma}$), and ii) sums of stochastic
701 elasticities with respect to the mean ($\Sigma E_{a_{ij}}^{S\mu}$). The first step of our framework shows the
702 variance compound of the sums of stochastic elasticities forming a continuum where the
703 right-hand side of the plot represents species (or populations) where a perturbation of
704 variance in demographic processes results in weak or no impact on λ_s (yellow dots). The
705 yellow-dotted species (or populations) can be classified as having potentially *buffered life-*
706 *cycles* – based on all the demographic processes. The left-hand side of the graph represents
707 species (or populations) where a perturbation of the variance in demographic processes
708 results in strong impact on λ_s (blue dots). Thus, the blue-dotted species (or populations) can
709 be classified as having potentially *unbuffered life cycles* – based on all the demographic
710 processes. The vertical axis delineates the values of the density distribution function,
711 indicating the number of species/populations at each value of $\Sigma E_{a_{ij}}^{S\sigma}$. The placement of data
712 points (species/populations) along the horizontal axis corresponds to their calculated values
713 of $\Sigma E_{a_{ij}}^{S\sigma}$ and is arranged linearly, while the breadth along the y-axis is solely for improved
714 visual comprehension. Step 2 - Access the linear selection pressures for individual species or
715 populations at within-species level (see text) (plot B). Step 2 displays the elasticities of the
716 deterministic population growth rate (λ_t) for a hypothetical population of wolf and reveals the
717 linear selection gradients, and which demographic processes are the most influential for λ_t .
718 Step 3 - Access the nonlinear selection pressures at the within-species level (see text) (plot

719 C). In the third step self-second derivatives for the corresponding demographic processes
720 from step 2 are displayed.

721

722 **Figure 2.** Results for step 1 of our framework showing the sum of stochastic elasticities with
723 respect to the variance $\Sigma E_{a_{ij}}^{S\sigma}$. The closer the $\Sigma E_{a_{ij}}^{S\sigma}$ is to zero, the weaker the impact of
724 variation in demographic processes on λ_s . The 40 populations from 34 species of mammals
725 from the COMADRE database are ranked into the variance continuum from potentially
726 buffered (right-hand side) to less buffered (left-hand side), since any variation in
727 demographic processes would strongly impact λ_s . Colors represent different taxonomic orders
728 with Primates occupying the right-hand side. Silhouettes: a) *Brachyteles hypoxantus*, b)
729 *Gorilla beringhei*, c) *Cercopithecus mitis*, d) *Urocitellus columbianus*, e) *Mustela erminea*, f)
730 *Erythrocebus patas*, g) *Lepus americanus*, h) *Rattus fuscipes*, i) *Ovis aries*, j) *Homo sapiens*,
731 k) *Macropus eugenii*, and l) *Felis catus*. The vertical axis delineates the values of the density
732 distribution function, indicating the number of species/populations at each value of $\Sigma E_{a_{ij}}^{S\sigma}$.
733 The placement of data points (species/populations) along the horizontal axis corresponds to
734 their calculated values of $\Sigma E_{a_{ij}}^{S\sigma}$ and is arranged linearly, while the breadth along the y-axis is
735 solely for improved visual comprehension.

736

737 **Figure 3:** Results from steps 2 and 3 of the proposed framework (see Fig. 2B, C). The 16
738 plots represent populations where the MPMs built by ages were available in the COMADRE
739 database (see text). The color scale represents elasticity values for each of the demographic
740 processes in the MPM, where yellow represents high and blue low elasticity values. No color
741 means elasticity=0. Because the aim of step 2 is to identify the most impacting demographic
742 process within each species' life cycle (the within-populations level, see text) - not to

743 compare the elasticity values among species - each plot has its own scale (see end of legend).
744 The black dots represent negative self-second derivatives of λ_t - thus concave selection - and
745 the white dots represent positive self-second derivatives of λ_t - thus convex selection. The dot
746 sizes are scaled by the absolute value of self-second derivatives, where the smaller the dot,
747 the closer a self-second derivative is to 0, indicating weak or no nonlinearity. Large dots
748 indicate strong nonlinear selection forces. Scales ($E_{\min-\max}$ =elasticity minimum and maximum
749 value, $SSD_{\min-\max}$ =self-second derivative minimum and maximum value): Blue monkey $E_{\min-$
750 $\max=0.00-0.52$, $SSD_{\min-\max}=-1.25-1.27$; Columbian ground squirrel: $E_{\min-\max}=0.00-0.23$,
751 $SSD_{\min-\max}=-1.48-0.01$; Eastern chimpanzee: $E_{\min-\max}=0.00-0.60$, $SSD_{\min-\max}=-4.39-2.59$;
752 Human: $E_{\min-\max}=0.00-0.18$, $SSD_{\min-\max}=-0.15-0.08$; Killer whale: $E_{\min-\max}=0.00-0.55$,
753 $SSD_{\min-\max}=-5.72-3.43$; Moose: $E_{\min-\max}=0.00-0.55$, $SSD_{\min-\max}=-0.66-0.36$; Mountain gorilla:
754 $E_{\min-\max}=0.00-0.81$, $SSD_{\min-\max}=-1.46-0.28$; Northern muriqui: $E_{\min-\max}=0.00-0.72$, $SSD_{\min-$
755 $\max=-1.17-0.35$; Olive baboon: $E_{\min-\max}=0.00-0.54$, $SSD_{\min-\max}=-0.57-1.13$; Polar bear: $E_{\min-$
756 $\max=0.00-0.26$, $SSD_{\min-\max}=-0.73-0.54$; Rhesus macaque: $E_{\min-\max}=0.00-0.51$, $SSD_{\min-\max}=-$
757 $0.54-0.71$; Root vole: $E_{\min-\max}=0.00-0.86$, $SSD_{\min-\max}=-2.54-0.22$; Soay sheep: $E_{\min-\max}=0.00-$
758 0.56 , $SSD_{\min-\max}=-0.22-0.40$; Tammar wallaby: $E_{\min-\max}=0.00-0.55$, $SSD_{\min-\max}=-0.64-0.34$;
759 White faced capuchin monkey: $E_{\min-\max}=0.00-0.66$, $SSD_{\min-\max}=-2.66-1.21$.

760

761 **Supplementary material – Data available in COMADRE Version 2.0.1 and results from Step 1 of the framework**

762 **Table S1.** The metadata used in step 1 of our framework and the respective results presented in the main text. The first four columns represent
763 the information from where Matrix Populations Models (MPMs) were extract precisely as presented in COMADRE 2.0.1. Column titles differ
764 from the database as “SpeciesAuthorComadre” is equivalent to “SpeciesAuthor” and “SpeciesName” is equivalent to “SpeciesAccepted” in
765 COMADRE 2.0.1. The remaining columns present the results of step 1, where we present the raw values of $\Sigma E_{aij}^{S\mu}$ and $\Sigma E_{aij}^{S\sigma}$, their respective
766 standard deviation, the stochastic population growth rate λ_s , and the number of available matrices (# matrices). For ByAge, “TRUE” was
767 assigned for MPMs built by age or “FALSE” if otherwise.

SpeciesAuthorComadre	SpeciesName	CommonName	Order	$\Sigma E_{aij}^{S\mu}$	$\Sigma E_{aij}^{S\mu}$ (sd)	$\Sigma E_{aij}^{S\sigma}$	$\Sigma E_{aij}^{S\sigma}$ (sd)	# matrices	λ
Homo_sapiens_subsp._sapiens	<i>Homo sapiens sapiens</i>	Human	Primates	1.003	0.003	1.003	0.004	13	1.064
Alces_alces	<i>Alces alces</i>	Moose	Artiodactyla	1.001	0.001	1.001	0.001	13	1.205
Antechinus_agilis	<i>Antechinus agilis</i>	Agile antechinus	Dasyuromorphia	1.111	0.111	1.111	0.011	2	0.931
Brachyteles_hypoxanthus	<i>Brachyteles hypoxanthus</i>	Northern muriqui	Primates	1.000	0.000	1.000	0.000	12	1.051
Callospermophilus_lateralis	<i>Callospermophilus lateralis</i>	Golden-mantled ground squirrel	Rodentia	1.054	0.054	1.054	0.055	9	2.052
Cebus_capucinus	<i>Cebus capucinus</i>	White faced capuchin monkey	Primates	1.000	0.000	1.000	0.000	11	1.021
Cercopithecus_mitis	<i>Cercopithecus mitis</i>	Blue monkey	Primates	1.000	0.000	1.000	0.000	14	1.036
Eumetopias_jubatus	<i>Eumetopias jubatus</i>	Northern sea lion; Steller sea lion	Carnivora	1.005	0.005	1.005	0.002	2	0.904
Felis_catus	<i>Felis catus</i>	Feral cat	Carnivora	1.136	0.136	1.136	0.012	1	1.948
Gorilla_beringei	<i>Gorilla beringei</i>	Mountain gorilla	Primates	1.000	0.000	1.000	0.000	21	1.027

Hippocamelus_bisulcus	<i>Hippocamelus bisulcus</i>	Huemul deer	Artiodactyla	1.002	0.002	1.002	0.001	1	0.996
Lepus_americanus	<i>Lepus americanus</i>	Snowshoe hare	Lagomorpha	1.294	0.294	1.294	0.165	2	0.812
Lycaon_pictus	<i>Lycaon pictus</i>	African wild dog	Carnivora	1.100	0.100	1.100	0.008	1	1.500
Macaca_mulatta_3	<i>Macaca mulatta</i>	Rhesus macaque	Primates	1.000	0.000	1.000	0.001	12	1.127
Macropus_eugenii	<i>Macropus eugenii</i>	Tammar wallaby	Diprotodontia	1.013	0.013	1.013	0.012	7	0.981
Marmota_flaviventris_2	<i>Marmota flaviventris</i>	Yellow-bellied marmot	Rodentia	1.007	0.007	1.007	0.006	4	0.890
Marmota_flaviventris_3	<i>Marmota flaviventris</i>	Yellow-bellied marmot	Rodentia	1.008	0.008	1.008	0.005	4	0.921
Microtus_oecconomus	<i>Microtus oecconomus</i>	Root vole	Rodentia	1.000	0.000	1.000	0.001	14	1.028
Mustela_erminea	<i>Mustela erminea</i>	Stoat	Carnivora	1.334	0.334	1.334	0.117	2	1.258
Orcinus_orca_2	<i>Orcinus orca</i>	Killer whale	Cetacea	1.001	0.001	1.001	0.001	24	0.999
Ovis_aries_2	<i>Ovis aries</i>	Soay sheep	Artiodactyla	1.033	0.033	1.033	0.020	3	1.099
Pan_troglodytes_subsp._schweinfurthii	<i>Pan troglodytes</i>	Eastern chimpanzee	Primates	1.000	0.000	1.000	0.001	22	0.982
Papio_cynocephalus	<i>Papio cynocephalus</i>	Olive baboon	Primates	1.000	0.000	1.000	0.000	19	1.054
Peromyscus_maniculatus_2	<i>Peromyscus maniculatus</i>	Deer mouse	Rodentia	1.010	0.010	1.010	0.005	2	1.107
Phocarctos_hookeri	<i>Phocarctos hookeri</i>	New Zealand sea lion	Carnivora	1.005	0.005	1.005	0.003	8	1.023
Propithecus_verreauxi	<i>Propithecus verreauxi</i>	Verreaux's sifaka	Primates	1.000	0.000	1.000	0.000	12	0.986
Puma_concolor_8	<i>Puma concolor</i>	Cougar	Carnivora	NA	NA	NA	NA	10	1.115
Rattus_fuscipes	<i>Rattus fuscipes</i>	Bush rat	Rodentia	1.246	0.246	1.246	0.029	2	1.305
Spermophilus_armatus	<i>Urocitellus armatus</i>	Uinta ground squirrel	Rodentia	1.016	0.016	1.016	0.011	4	1.125
Spermophilus_armatus_2	<i>Urocitellus armatus</i>	Uinta ground squirrel	Rodentia	1.017	0.017	1.017	0.010	3	1.095

Spermophilus_columbianus	<i>Urocitellus columbianus</i>	Columbian ground squirrel	Rodentia	1.036	0.036	1.036	0.025	3	1.009
Spermophilus_columbianus_3	<i>Urocitellus columbianus</i>	Columbian ground squirrel	Rodentia	1.003	0.003	1.003	0.006	3	1.200
Ursus_americanus_subsp._floridanus	<i>Ursus americanus</i>	Florida black bear	Carnivora	1.003	0.003	1.003	0.003	2	1.020
Ursus_arctos_subsp._horribilis_5	<i>Ursus arctos</i>	Grizzly bear	Carnivora	1.001	0.001	1.001	0.001	4	1.026
Ursus_maritimus_2	<i>Ursus maritimus</i>	Polar bear	Carnivora	1.019	0.019	1.019	0.007	2	0.941
Brachyteles_hypoxanthus_2	<i>Brachyteles hypoxanthus</i>	Northern muriqui	Primates	1.000	0.000	1.000	0.000	12	1.111
Cebus_capucinus_2	<i>Cebus capucinus</i>	WhiteNAfaced capuchin monkey	Primates	1.000	0.000	1.000	0.000	11	1.059
Chlorocebus_aethiops_2	<i>Chlorocebus aethiops</i>	Vervet	Primates	1.075	0.075	1.075	0.087	5	1.187
Erythrocebus_patas	<i>Erythrocebus patas</i>	Patas monkey	Primates	1.051	0.051	1.051	0.038	5	1.128
Gorilla_beringei_subsp._beringei	<i>Gorilla beringei</i>	Mountain gorilla	Primates	1.000	0.000	1.000	0.000	21	1.053
768									
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1 **A unified framework to identify demographic buffering in natural populations**

2 A manuscript in preparation for submission to ECOLOGY LETTERS

3 Type of article: METHOD

4
5 Gabriel Silva Santos^{1,2*}, Samuel J L Gascoigne^{3*}, André Tavares Corrêa Dias⁴, Maja Kajin
6^{3,5**♦}, Roberto Salguero-Gómez^{3♦}

7
8 1 National Institute of the Atlantic Forest (INMA), 29650-000, Santa Teresa, Espirito Santo,
9 Brazil. ssantos.gabriel@gmail.com

10 2 Department of Ecology, Graduate Program in Ecology and Evolution, Rio de Janeiro
11 State University, 524 São Francisco Xavier street, 20550-900, Maracanã, Rio de Janeiro,
12 Brazil

13 3 Department of Biology, University of Oxford, South Parks Road, OX1 3RB, Oxford, UK.
14 samuel.gascoigne@pmb.ox.ac.uk, rob.salguero@biology.ox.ac.uk,
15 maja.kajin@biology.ox.ac.uk

16 4 Department of Ecology, Institute of Biology, Universidade Federal do Rio de Janeiro,
17 Avenida Carlos Chagas Filho 373, 21941-590 Rio de Janeiro, RJ, Brazil. atcdias@gmail.com

18 5 Department of Biology, Biotechnical Faculty, University of Ljubljana, Večna pot 111, 1000
19 Ljubljana, Slovenia

20
21 *Shared first authorship

22 **Corresponding author

23 ♦Shared senior authorship

24
25 AUTHOR CONTRIBUTIONS: GSS developed the initial concept, performed the statistical
26 analyses and contributed to the first draft of the manuscript. SJLG developed the initial
27 concept, contributed to the first draft and all other versions of the manuscript and generated
28 final figures. ATCD co-advised the project and contributed significantly to final versions of
29 the manuscript. MK developed and managed the project, contributed to the first draft and all
30 other versions of the manuscript and generated final figures. RSG developed and managed
31 the project and contributed to the first draft and all other versions of the manuscript. All
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50 **Abstract** (146/150 words)

51 The Demographic Buffering Hypothesis (DBH) predicts that natural selection reduces the
52 temporal fluctuations in demographic processes (such as survival, development, and
53 reproduction), due to their negative impacts on population dynamics. However, a
54 comprehensive approach that allows for the examination of demographic buffering patterns
55 across multiple species is still lacking. Here, we propose a three-step framework aimed at
56 identifying and quantifying demographic buffering. Firstly, we categorize species along a
57 continuum of variance based on their stochastic elasticities. Secondly, we examine the linear
58 selection gradients, followed by the examination of nonlinear selection gradients as the third
59 step. With these three steps, our framework overcomes existing limitations of conventional
60 approaches to identify and quantify demographic buffering, allows for multi-species
61 comparisons, and offers insight into the evolutionary forces that shape demographic
62 buffering. We apply this framework to mammal species and discuss both the advantages and
63 potential of our framework.

64

65

66

67 Environmental stochasticity plays a pivotal role in shaping organisms' life histories (Bonsall
68 & Klug 2011). Nonetheless, how organisms will cope with the increasing variation in
69 environmental conditions expected under climate change (Boyce *et al.* 2006; Morris *et al.* 2008)
70 is one of the most intriguing questions of ecology and evolution (Sutherland *et al.* 2013).
71 Evolutionary demography offers a wide array of explanations for the evolutionary processes
72 that shape the diversity of demographic responses to environmental stochasticity
73 (Charlesworth 1994; Pfister 1998; Tuljapurkar *et al.* 2009; Healy *et al.* 2019; Hilde *et al.* 2020). The
74 Demographic Buffering Hypothesis (*DBH*, hereafter) (Morris & Doak 2004; Pélabon *et al.* 2020)
75 predicts a negative relationship between the contribution of a demographic processes (*e.g.*,
76 survival, development, reproduction) to the population growth rate (λ) and their temporal
77 variance (Pfister 1998). The emerging demographic strategy, demographic buffering,
78 accommodates variance of demographic processes to cope with the otherwise negative effects
79 of stochastic environments on λ (Pfister 1998; Morris & Doak 2004; Hilde *et al.* 2020).

80 A unified approach to unambiguously quantify demographic buffering is still missing.
81 Indeed, identifying demographic buffering remains challenging (Morris & Doak 2004; Doak *et*
82 *al.* 2005) for at least three reasons. First is the different interpretation of results from
83 correlational analyses (*e.g.*, as in Pfister, 1998). Some authors have used the correlation
84 coefficient as an index to order species' life histories in a continuum ranging from buffered
85 (Spearman's correlation $\rho = <0$ between the sensitivity of λ to demographic processes and
86 their temporal variance) to labile ($\rho = >0$, regardless of the "scatterness" around the
87 regression (McDonald *et al.* 2017). In contrast, other researchers interpret the absence of
88 statistical support for demographic buffering as an alternative strategy where variance in
89 demographic process(es) is favoured to track environmental conditions (the so-called
90 Demographic Lability Hypothesis (*DLH*, hereafter; *e.g.*, (Koons *et al.* 2009; Reed & Slade 2012;
91 Jäkäläniemi *et al.* 2013; Hilde *et al.* 2020).

92 The second obstacle to obtain generalisation across species' populations regarding
93 demographic buffering is the hierarchical level at which this phenomenon is typically
94 examined. Some studies base their investigations of demographic buffering on the *whole* life
95 history at the level of species or populations (*interspecific level*, hereafter), focusing on the
96 one demographic process that is the most influential for λ (Reed & Slade 2012; McDonald *et al.*
97 2017). At the interspecific level, a life history is referred to as demographically buffered if the
98 most important demographic process has low temporal variance (Pfister 1998; Morris & Doak
99 2004; Hilde *et al.* 2020; Le Coeur *et al.* 2022). Thus, the associated strategy is commonly
100 decided based on a *single* demographic process (*e.g.*, adult survival), ignoring the selection
101 pressures on the rest of the demographic processes within the life cycle. However, to
102 understand how, why, and where demographic buffering occurs –or not– and how buffering
103 patterns might be modified in response to the environment, it is essential to also consider the
104 features *within* a single species' life cycle (*intraspecific level*, hereafter). Within a single life
105 cycle one demographic process can be buffered against while another can be labile to the
106 environment – supporting the DLH (Koons *et al.* 2009; Jongejans *et al.* 2010; Barraquand &
107 Yoccoz 2013). Thus, for a mechanistic understanding of how environmental stochasticity
108 shapes life histories, both inter- and intra-specific levels need to be addressed.

109 The third reason limiting a holistic understanding of demographic strategies in
110 stochastic environments are the challenges inherent to examining their underlying
111 mechanisms. Evidence for demographic buffering exists across some long-lived organisms
112 with complex life cycles, (Pfister 1998; Gaillard & Yoccoz 2003; Doak *et al.* 2005; Rotella *et al.*
113 2012; McDonald *et al.* 2017), but also in short-lived species (Pfister 1998; Reed & Slade 2012;
114 Ferreira *et al.* 2013). Importantly, these patterns of variation do not inform on how the life
115 histories were shaped by natural selection. To do so, one would need to identify the type
116 (linear or nonlinear) and strength of selection acting on demographic processes. Linear

117 selection acts on changing *the mean* value of a demographic process via a linear function
118 between the fitness and the demographic process. In contrast, nonlinear selection acts on *the*
119 *variance* of demographic processes either increasing it, decreasing it, or
120 increasing/decreasing *the covariance* between two demographic processes (Brodie et al.
121 1995; Carslake et al. 2008).

122 The sign of the self-second derivative of λ determines the type of nonlinear selection
123 acting on a demographic process. For instance, a negative self-second derivative for a given
124 demographic process describes a concave form of selection, commonly referred to as the \cap -
125 shaped selection (Caswell 1996, 2001; Shyu & Caswell 2014). This form of selection reduces the
126 temporal variance in said demographic process, thereby providing support for the DBH.
127 Conversely, a demographic process yielding a positive self-second derivative identifies a
128 convex, or U-shaped selection (Caswell 1996, 2001; Shyu & Caswell 2014). Such a selection
129 mechanism acts upon demographic processes amplifying their temporal variance, thus
130 supporting the DLH (Koons *et al.* 2009; Le Coeur *et al.* 2022). The cross-second derivatives (not
131 discussed here, see Caswell 1996, 2001 for further details) quantify selection pressures acting
132 on the strength of correlation among different demographic processes.

133 The rich variation in demographic strategies across the Tree of Life is a result of
134 evolutionary processes that have shaped variance in demographic processes through time. In
135 this context, setting demographic buffering into the adaptive landscape context of linear and
136 nonlinear selection enables us to identify and quantify the evolutionary processes that
137 generate said demographic patterns. In this way, one will better understand how increased
138 variability of environmental conditions might act on the existing –and shape novel–
139 demographic strategies. However, we still lack a unified approach to quantify DBH.

140 Here, we present a framework that identifies and quantifies demographic buffering.
141 Our framework provides a thorough analysis of temporal variance in demographic processes

142 affected by environmental stochasticity. This framework involves categorizing species or
143 populations along a variance continuum based on the extent to which key demographic
144 processes are buffered by natural selection, thereby limiting their temporal variability. The
145 framework consists of four steps with a mix of well-known methods applied to stage-
146 structured demographic information (*e.g.*, matrix population models [Caswell 2001]; integral
147 projection models [Easterling et al. 2000]). First, we position species or populations on the
148 aforementioned continuum to assess the cumulative effect of the variance on their key
149 demographic processes at the interspecific level (see below). Second, we investigate the
150 presence of linear selection forces operating within the life cycle of each species or
151 population at the intraspecific level (below). Third, we explore the impact of non-linear
152 selection forces acting within the life cycle of each species or population, also at the
153 intraspecific level. The combination of these three steps provides quantitative evidence
154 for/against the DBH, while in step four we describe how to test the DLH.

155 To demonstrate the applicability of our framework, we apply it to 40 populations of
156 34 mammal species sourced from the COMADRE database (Salguero-Gómez *et al.* 2016). We
157 showcase how the framework can provide valuable insights into the patterns of demographic
158 buffering across species. The framework offers novel, detailed insights into the selection
159 pressures that act *within* species' life cycles, thus allowing for a thorough understanding of
160 the evolutionary selection forces that shape the patterns of demographic buffering across
161 species. Beyond providing a quantitative, systematic toolset to test the DBH through three
162 steps, we have also offer an alternative fourth step that briefly outlines how to test for the
163 DLH.

164

165 A unified framework to assess evidence of DBH

166 The evidence for demographic buffering has been mainly assessed using Matrix
167 Population Models (Pfister 1998; Rotella *et al.* 2012). However, Integral Projection Models
168 (IPM; Rodríguez-Caro *et al.* 2020; Wang *et al.* 2023) can be equally applied for identifying
169 the demographic buffering signatures. Both MPMs and IPMs are stage-structured, discrete-
170 time demographic models (Caswell 2001; Ellner *et al.* 2016). For simplicity, here we focus on
171 MPMs, but note that the same approaches are as equally applicable to IPMs (Griffith 2017;
172 Doak *et al.* 2021). Throughout this manuscript, we refer to demographic processes as both
173 matrix entries a_{ij} (*i.e.*, upper-level parameters) and the vital rates that underlie the matrix
174 elements (*i.e.*, lower-level parameters), and note that their conversion is straightforward and
175 described elsewhere (Franco & Silvertown 2004). The framework operates on three steps:

176 The first step of our framework involves acquiring the relative contribution of each
177 demographic process to the stochastic growth rate, λ_s , the so-called stochastic elasticities, E_{ij}^S
178 (Tuljapurkar *et al.* 2003) (Figure 1A). The sum of all stochastic elasticities ($\Sigma E_{a_{ij}}^S$), can be
179 separated into two components to assess how temporal variance and mean values of each
180 demographic process contributes to λ_s . The first component represents the *sum of stochastic*
181 *elasticity of λ_s with respect to the variance* $\Sigma E_{a_{ij}}^{S\sigma}$, and the second represents the *sum of*
182 *stochastic elasticity of λ_s with respect to the mean* $\Sigma E_{a_{ij}}^{S\mu}$, where $\Sigma E_{a_{ij}}^S = \Sigma E_{a_{ij}}^{S\sigma} + \Sigma E_{a_{ij}}^{S\mu}$. Thus,
183 the summation $\Sigma E_{a_{ij}}^{S\sigma}$ quantifies the extent to which the stochastic population growth rate (λ_s)
184 is influenced by changes in the variances of the demographic processes within the population
185 matrix.

186 A higher sum of stochastic elasticity of λ_s with respect to the variance (*i.e.*, higher
187 absolute value; $|\Sigma E_{a_{ij}}^{S\sigma}|$) indicates that small changes in the variance of demographic processes
188 would have a substantial impact on λ_s . In other words, the variance of that demographic

189 process is not constrained by selection, supporting the DLH. On the other hand, a lower
190 (absolute) stochastic elasticity of λ_s with respect to the variance suggests that λ_s is less
191 sensitive to such perturbations, or, that variance of such demographic process is being
192 constrained by natural selection, supporting the DBH (Tuljapurkar *et al.* 2003; Haridas &
193 Tuljapurkar 2005) (Fig. 1A).

194 The first step of the framework thus features the interspecific level and places species
195 or populations alongside a continuum. Species exhibiting unconstrained variance in the most
196 important demographic process (*i.e.*, not buffered/potentially DLH suggesting, Fig. 1A, blue
197 dots) are positioned on the left-hand side of the continuum. In contrast, species with
198 constrained variance in the most important demographic process (*i.e.*, supporting the DBH,
199 Fig. 1A, yellow dots) are positioned on the right-hand side of the continuum. However, the
200 left-hand side of the continuum does not necessarily imply evidence of demographic lability.
201 This is so because demographic lability is defined as an increase in the *mean value* of a
202 demographic process in response to improved environmental conditions (Le Coeur *et al.* 2022).
203 By examining $\Sigma E_{a_{ij}}^{S\sigma}$, we can visualize an increase or decrease in *variance* of demographic
204 processes, while the mean value of a demographic process does not change. The right-hand
205 side (near 0 values for $\Sigma E_{a_{ij}}^{S\sigma}$) supports the DBH, while the opposite end represents the lack
206 of support for the DBH, and potentially support for the DLH. However, to undoubtedly
207 provide support for the DLH, further investigation of demographic parameters is needed, as
208 described below.

209 Step 1 of our framework examines the impacts that environmental variation has on the
210 long-term population growth rate, λ_s (Tuljapurkar *et al.* 2003). This means that the resulting
211 variance continuum in this step of the framework is based on how λ_s was affected by
212 variation in the key demographic parameter across all contiguous time periods.

213 Steps 2 and 3 of the framework are conducted at the intraspecific level. Once species
214 or populations are positioned along the variance continuum regarding the most important
215 demographic process for λ_s , (step 1), one needs to zoom into each life cycle separately,
216 analysing the selection pressures acting on each one of the demographic processes composing
217 the life cycle. In doing so, one can inspect the selection pressures that have generated the
218 patterns found in step 1. Step 2 (Fig. 1B) requires obtaining the partial derivatives of the
219 deterministic population growth rate, λ_t , relative to all matrix elements of the MPM of interest
220 (*i.e.*, elasticities of λ_t w.r.t each demographic process in the MPM). Step 2 therefore informs
221 on the strength of the natural selection on each of the demographic processes.

222 Finally, in step 3, one assesses the pattern of nonlinear selection by using the self-
223 second derivatives of λ_t with respect to each demographic process (Fig. 1C). This final step
224 reveals the potential nonlinear selection pressures on all the demographic processes within a
225 life cycle, rather than only the most important one. This final step is key to understanding the
226 evolutionary processes (*i.e.*, types of nonlinear selection) that the demographic processes are
227 subjected to. Without understanding the evolutionary processes operating on the demographic
228 processes, the pattern observed in step 1 might be artefactual. Moreover, step 1 is founded on
229 the assumption that the importance of a demographic process, as indicated by its elasticity,
230 remains unchanged over time. However, stochastic environments can substantially alter
231 elasticity patterns throughout a life cycle (e.g., Lawler et al. 2009).

232 Steps 2 and 3 of the framework feature selection pressures that have been averaged
233 over the contiguous time periods. This means that the resulting patterns are based on how λ_t
234 (obtained from averaging all sequential MPMs across the duration of the study) would be
235 affected if a demographic process were perturbed. Therefore, steps 2 and 3 are based on a
236 different information than step 1, and can thus complete our understanding of the role of
237 selection pressures on shaping demographic patterns across multiple species.

238 Another important asset of step 3 above includes the notion that the relative
239 importance (elasticity) of demographic processes themselves changes with changing
240 environment (Stearns 1992). In other words, the extent to which λ_t is sensitive to
241 perturbations in a specific demographic process is *dynamic* (Kroon, Hans *et al.* 2000). Thus, the
242 self-second derivatives generate information on how the sensitivity (or elasticity) of λ_t –
243 based on which the entire variance continuum of species is produced in step 1 – might
244 change. If the sensitivity (or elasticity) of λ_t can change, then it is important to know which
245 demographic processes are most prone to trigger such a change. In the example of a
246 hypothetical wolf species (Fig. 1), this means that if the reproduction of the third age-class
247 individuals (matrix element $a_{1,3}$) decreased, the sensitivity of λ_t to $a_{1,3}$ would increase (square
248 with the largest black dot, Fig. 1C). Consequently, with increased environmental variability,
249 the key demographic process used to place this species onto the variance continuum in step 1
250 might change from remaining in the fourth age class (matrix element $a_{4,4}$, Fig. 1B) to
251 reproduction of the third age-class (matrix element $a_{1,3}$, Fig. 1C).

252 Combining the three steps of our framework allows for the clear, quantitative, holistic
253 identification of evidence to support (or reject) the DBH. Steps 2 and 3 offer key insights as
254 to *why* a given species or population is placed on either the buffered or the non-buffered
255 (potentially labile) end of the variance continuum. A clear and unequivocal evidence for
256 support towards the DBH consists of: (1) a species or population being positioned near the 0
257 end of the continuum (the right-hand side) in step 1; (2) this species' or populations' life
258 cycle having one or more demographic processes with highest elasticity values in step 2; and
259 (3) the same demographic process displaying the highest elasticity in step 2 with negative
260 self-second derivative values in step 3. In this sense, Figure 1B shows that, for the chosen
261 population of a hypothetical wolf species, the most important demographic process is
262 remaining in the fourth stage (MPM element $a_{4,4}$), as this demographic process results in

263 highest elasticity value (Fig. 1B yellow square). However, Fig. 1C reveals that $a_{4,4}$ is under
264 little selection pressure for variance reduction. Thus, there is no evidence for DBH from the
265 third step of the framework (*i.e.*, no concave selection forces), therefore, the lack of concave
266 selection forces on the key demographic process within wolf's life cycle explains why this
267 species is placed on the left-hand side of the variance continuum (Fig. 1A).

268 Species placed on the non-buffered end of the continuum is the first but not last step
269 to evidence demographic lability. Indeed, locating a species on the non-buffered end of the
270 variance continuum is a necessary but not sufficient condition for evidence in favour of the
271 DLH. It is key highlighting here that demographic buffering and lability do not represent two
272 extremes of the same continuum. The variance continuum allocates the species or populations
273 from strongly buffered to non-buffered, but to test the DLH, a further step is needed.

274 Although not our primary goal here, we briefly introduce said step 4. To establish
275 compelling evidence for or against the DLH, it is essential to fulfil several criteria. First,
276 sufficient data across various environments (over time or space) are required to construct
277 reaction norms that depict how a demographic process responds to environmental changes
278 (Morris et al., 2008; Koons et al., 2009). Second, non-linear relationships between
279 demographic processes and the environment must be established based on these reaction
280 norms. Lastly, to identify demographic processes where an increase in the mean value has a
281 stronger positive impact on population growth rate than the detrimental effect of increased
282 variance. This latter condition is only achieved when the vital rate-environment reaction
283 norm is convex (U-shaped; Morris et al. 2008; Koons et al. 2009). Importantly, we note that
284 more likely than previously thought (*e.g.*, Pfister 1998), species do not exist as purely
285 buffering or labile, but that within species, some vital rates may be buffered, other labile, and
286 others insensitive to the environment (*e.g.*, Doak et al. 2005). Deciphering generality in this
287 likely complex pattern should attract much research attention going forward, in our opinion.

288

289 **Demographic buffering in mammals: a case study using the unified framework**

290 We demonstrate the performance of our framework using 44 MPMs from 34 mammal
291 species. Mammals are of special interest here for two reasons: (1) mammalian life histories
292 have been well studied (Gillespie 1977; Stearns 1983; Bielby *et al.* 2007; Jones 2011); and (2)
293 some of their populations have already been assessed in terms of buffering, particularly for
294 primates (Morris *et al.* 2008, 2011; Reed & Slade 2012; Rotella *et al.* 2012; Campos *et al.* 2017).
295 Together, the well-studied life histories and previous information about the occurrence of
296 buffering in mammals provide the necessary information to make accurate predictions and
297 validate the performance of the proposed framework.

298 We used Matrix Population Models from 40 out of 139 studies with mammals
299 available in the COMADRE database v.3.0.0 (Salguero-Gómez *et al.* 2016). These 40
300 populations encompass 34 species from eight taxonomic orders. We included these MPMs in
301 our analyses because they provide values of demographic processes (a_{ij}) for three or more
302 contiguous time periods, thus allowing us to obtain the stochastic elasticity of each a_{ij} .
303 Although we are aware that not all possible temporal variation in demographic processes may
304 have been expressed within this period, we assumed three or more transitions are enough to
305 provide sufficient variation for population comparison. At least three contiguous time periods
306 - a common selection criteria in comparative studies of stochastic demography (Compagnoni
307 *et al.* 2023) - also allowed to test and showcase our framework. Fortunately, several long-lived
308 species, characterized by low variation in their demographic processes, were studied for a
309 long time (*e.g.*, some primates in our dataset have been studied for over 20 years – Morris *et*
310 *al.* 2011). We removed the populations where either only survival or only reproduction rates
311 were reported, because of the impossibility to calculate the stochastic growth rate. A detailed
312 description of the analysed data and their original sources are available in supplementary
313 material (Supplementary Material, Table S1).

314 *Homo sapiens* was included in our analyses because it is the only mammalian species
315 in which second-order derivatives have been applied (Caswell 1996). Therefore, *Homo*
316 *sapiens* provides an ideal basis for comparisons among species. The data for *Homo sapiens*
317 were gathered from 26 modern populations located in various cities, allowing us to construct
318 a spatiotemporal variance. It is important to note that in this case, we are not working with
319 true temporal variance but rather a variance that encompasses both spatial and temporal
320 aspects.

321 For steps 2 and 3 of our framework, we utilized a subset of 16 populations (including
322 *Homo sapiens*) whose population projection matrices (MPMs) were organized by age. We
323 specifically selected these populations because their life cycles can be summarized by two
324 main demographic processes: survival and contribution to recruitment of new individuals.
325 The contribution to recruitment can be interpreted as either the mean reproductive output for
326 each age class or an approximation thereof, depending on how the matrices are structured
327 (Ebert 1999). One advantage of using such matrices is that they encompass only two types of
328 demographic processes, namely survival and recruitment, eliminating the need to account for
329 multiple transitions between different life stages.

330 To perform the step 1 of our framework and obtain the $\Sigma E_{a_{ij}}^{S\sigma}$ (and $\Sigma E_{a_{ij}}^{S\mu}$), we followed
331 Tuljapurkar *et al.* (2003). To perform step 2 of our framework, we calculated the
332 deterministic elasticities of each demographic process extracted using the *popbio* package.
333 All analyses were performed using R version 3.5.1 (R Core team, 2018). Finally, to perform
334 the step 3 of our framework the self-second derivatives were adapted from *demogR* (Jones
335 2007) following Caswell 1996 and applied for the mean MPM.

336 *Results*

337 We ranked 40 populations from the 34 identified mammal species according to the
 338 cumulative impact of variation in demographic processes on λ_s using the step 1 of our
 339 framework (Fig. 2). Additional information is provided in the supplementary material (Table
 340 S1). Most of the analysed orders were placed on the low-variance end of the variance
 341 continuum (Fig. 2). The smallest contributions of variation in demographic processes (*i.e.*,
 342 maximum value of $\Sigma E_{a_{ij}}^{S\sigma}$, note that $\Sigma E_{a_{ij}}^{S\sigma}$ ranges from 0 to -1), suggesting more buffered
 343 populations, were assigned to Primates: northern muriqui (*Brachyteles hypoxantus*, $\Sigma E_{a_{ij}}^{S\sigma} = -$
 344 $0.09 \times 10^{-4} \pm 0.12 \times 10^{-4}$) (mean \pm standard deviation) (Fig. 2 silhouette a), mountain gorilla
 345 (*Gorilla beringhei*, $\Sigma E_{a_{ij}}^{S\sigma} = -0.24 \times 10^{-4} \pm 0.08 \times 10^{-4}$) (Fig. 2 silhouette b), followed by the
 346 blue monkey (*Cercopithecus mitis*, $\Sigma E_{a_{ij}}^{S\sigma} = -0.63 \times 10^{-4} \pm 0.06 \times 10^{-4}$) (Fig. 2 silhouette c).
 347 The first non-primate species placed near the low-variance end of the continuum was the
 348 Columbian ground squirrel (*Urocitellus columbianus*, Rodentia, $\Sigma E_{a_{ij}}^{S\sigma} = -0.003 \pm 0.002$) (Fig.
 349 2 silhouette d). The species with the highest contribution of variation in demographic
 350 processes placed at the high-variance end of the continuum was the stoat (*Mustela erminea*,
 351 Carnivora, $\Sigma E_{a_{ij}}^{S\sigma} = -0.35 \pm 0.02$) (Fig. 2 silhouette e). All the 14 primate populations
 352 supported the DBH, occupying the right-hand side of the variance continuum, with exception
 353 of the Patas monkey (*Erythrocebus patas*, Primates, $\Sigma E_{a_{ij}}^{S\sigma} = -0.05 \pm 0.03$) (Fig. 2 silhouette
 354 f). The snowshoe hare (*Lepus americanus*, Lagomorpha, $\Sigma E_{a_{ij}}^{S\sigma} = -0.29 \pm 0.16$) (Fig. 2
 355 silhouette g) and the Bush rat (*Rattus fuscipes*, Rodentia, $\Sigma E_{a_{ij}}^{S\sigma} = -0.25 \pm 0.03$) (Fig. 2
 356 silhouette h) appear on the high-variance end of the continuum.

357 As predicted for the steps 2 and 3, we could not observe a clear pattern in support of
 358 the DBH. This finding means that the demographic processes with the highest elasticity
 359 values failed to display strongly negative self-second derivatives (Fig. 3). Particularly for

360 majority of primates - with the lack or minor temporal variation in demographic processes -
361 demographic processes with high elasticities had positive values for the self-second
362 derivatives (indicated by yellow squares with white dots in Fig. 3). Examples of primate
363 species exhibiting high elasticities and positive values for the self-second derivatives and
364 include northern muriqui (*Brachyteles hypoxanthus*), mountain gorilla (*Gorilla beringei*),
365 white-faced capuchin monkey (*Cebus capucinus*), rhesus monkey (*Macaca mulatta*), blue
366 monkey (*Cercopithecus mitis*), Verreaux's sifaka (*Propithecus verreauxi*) and olive baboon
367 (*Papio cynocephalus*) (Fig. 3). This implies that the key demographic processes influencing
368 λ_t are not subject to selective pressure for reducing their temporal variability. However, even
369 though the primates were positioned closer to the low-variance end of the continuum in step
370 1, the evidence from steps 2 and 3 does not support DBH.

371 The killer whale showed similar controversy between step 1 and steps 2-3 results as
372 most primates. In step 1, the killer whale was positioned at the buffered end of the variance
373 continuum (*Orcinus orca*, Cetacea, $\Sigma E_{a_{ij}}^{S\sigma} = -0.70 \times 10^{-4} \pm 1.04 \times 10^{-5}$) (Fig. 2 silhouette not
374 shown). However, steps 2 and 3 show that the three demographic processes in killer whale
375 life cycle with highest elasticity values (matrix elements $a_{2,2}$, $a_{3,3}$ and $a_{4,4}$) are not under
376 selection pressures for reducing their temporal variance, but the opposite (depicted by yellow
377 and green squares with white dots, Fig. 3).

378 The only primate species exhibiting DBH evidence in steps 2 and 3 was human. In
379 human, demographic parameters representing survival from first to second age class (matrix
380 element $a_{2,1}$) displayed high elasticities and negative self-second derivatives (depicted as
381 yellow squares with black dots in Fig. 3). Evidence supporting the DBH was also found in
382 the Columbian ground squirrel (*Urocitellus columbianus*), where, similar to humans, survival
383 from the first to the second age class (matrix element $a_{2,1}$) showed indications of selection
384 acting to reduce its variance. Accordingly, the Columbian ground squirrel was positioned

385 close to the buffered end of the variance continuum in step 1. Hence, the Columbian ground
386 squirrel was the sole species with consistent DBH support across all three steps of the
387 framework.

388 The Soay sheep (*Ovis aries*) was the species furthest from the buffered end of the
389 variance continuum that enabled to perform steps 2 and 3. For the Soay sheep, remaining in
390 the third age class (matrix element $a_{3,3}$) has the major influence on λ_t and is under selection
391 pressure to have its variance increased. The latter characteristics reveal conditions for the
392 DLH support even though the species is placed closer to the buffered end of the variance
393 continuum.

394 Steps 2 and 3 illustrate the importance of examining DBH evidence on the
395 intraspecific level. These two steps of the framework identify the simultaneous acting of
396 concave and convex selection on different demographic processes but within a single life
397 cycle. In polar bear (*Ursus maritimus*), the key demographic process (matrix element $a_{4,4}$) is
398 under convex selection, as depicted by a yellow square with a white dot in Fig. 3. However,
399 the demographic process with the second highest elasticity value (matrix element $a_{5,4}$) is
400 under strong concave selection (depicted by a light green square with a black dot in Fig. 3).

401 By adding step 3 to the framework, another important information was added. The
402 high absolute values of self-second derivatives (large dots, either black or white, Fig. 3)
403 indicate where the sensitivity of λ_t to demographic parameters is itself prone to environmental
404 changes. For instance, if the value of $a_{5,4}$ for polar bear increased, the sensitivity of λ_t to $a_{5,4}$
405 would decrease because the self-second derivative of $a_{5,4}$ is highly negative (depicted by the
406 largest black dot in polar bear MPM). Vice versa holds for the $a_{4,4}$ demographic process,
407 where an increase in the value of $a_{4,4}$ would increase λ_t 's sensitivity to $a_{4,4}$, because the self-
408 second derivative of $a_{5,4}$ is highly positive (depicted by the largest white dot in polar bear

409 MPM). Thus, sensitivities (or equally elasticities) of demographic processes with high
410 absolute values for self-second derivatives can easily change - potentially changing the key
411 demographic process used for allocating species into the variance continuum in step 1 of the
412 framework.

413 **Discussion**

414 In the Anthropocene, identifying and quantifying mechanisms of species responses to
415 stochastic environments holds crucial importance. This importance is particularly tangible in
416 the context of the unprecedented environmental changes and uncertainties that impact the
417 dynamics and persistence of natural populations (Boyce *et al.* 2006). Correlational
418 demographic analysis, whereby the importance of demographic processes and their temporal
419 variability is examined (e.g., Pfister 1998), has attempted to identify how species may buffer
420 against the negative effects of environmental stochasticity. However, these widely used
421 approaches have important limitations (see Introduction and Hilde *et al.* 2020). Our novel
422 framework overcomes said limitations by providing a rigorous approach to test the
423 demographic buffering hypothesis (DBH; Pfister 1998; Hilde *et al.* 2020).

424 Evidencing demographic buffering is not straightforward. Indeed, through the
425 analysis of stochastic population growth rate (λ_s) in our application of the framework to 44
426 populations of 34 species, we identify the highest density of natural populations near the
427 buffered end of the variance continuum (step 1), indicating possible support for the DBH.
428 However, we show that the same species then fail to exhibit signs of concave (\cap -shaped)
429 selection on the key demographic parameters when further analyses are performed averaging
430 the variation across the duration of each study (steps 2 and 3). This finding confirms that
431 placing the species near the buffered end of the variance continuum is *necessary* but not
432 *sufficient* to test the DBH. Indeed, buffering occurs when concave selection forces act on the
433 key demographic parameter (Caswell 1996, 2001; Shyu & Caswell 2014).

434 Combining the three steps into a unified framework is of utmost importance. In steps
435 2 and 3 of the framework, we find relatively limited overall support for the DBH in the
436 examination of our 16 (out of 34 in step 1) studied animal species. Step 3 of our framework
437 reveals that the role of natural selection shaping temporal variation in demographic processes
438 is more complex than expected by the DBH alone. Indeed, demographic processes within our
439 study populations are often under a mix of convex and concave selection. This mix of
440 selection patterns was already suggested by Doak *et al.* (2005). Here, only two out of 16
441 mammal species revealed concave selection acting on the key demographic processes
442 (Columbian ground squirrel [*Urocitellus columbianus*], and humans, [*Homo sapiens*
443 *sapiens*]). These two species were also placed near the buffered end of the variance
444 continuum, therefore meeting all the necessary conditions to diagnose clear support in favour
445 of DBH. However, finding 12.5% (two out of 16) species that meet the criteria for
446 demographic buffering is not in concordance with previous studies. Support for the DBH has
447 been reported across 22 ungulate species (Gaillard & Yoccoz 2003). In the one ungulate we
448 examined, the moose (*Alces alces*), we find only partial support for DBH in adult survival,
449 since this species is placed near the buffered end of the variance continuum in step 1 but does
450 not show concave selection pressures on adult survival in step 2/3, as predicted by the DBH.

451 Our overall findings reveal varying levels of support for the notion that adult survival
452 in long-lived species tends to be buffered. Indeed, Gaillard *et al.* (1998) found that adult
453 female survival varied considerably less than juvenile survival in large herbivores. This
454 finding was also supported by further studies in ungulates (Gaillard & Yoccoz 2003), turtles
455 (Heppell 1998), vertebrates and plants (Pfister 1998), and more recently across nine (out of
456 73) species of plants (McDonald *et al.* 2017).

457 When placing our study species along a variance continuum (step 1), primates tend to
458 be located on the buffered end. However, most primates displayed convex –instead of the

459 expected concave– selection on adult survival. Similar results, where the key demographic
460 process failed to display constrained temporal variability, have been reported for long-lived
461 seabirds (Doherty *et al.* 2004). One explanation for the unexpected convex selection on adult
462 survival involves trade-offs, as suggested by Doak *et al.* (2005). When two demographic
463 parameters are negatively correlated, the variance of population growth rate (λ) can be
464 increased or decreased (Evans & Holsinger 2012; Compagnoni *et al.* 2016). The well-established
465 trade-off between survival and fecundity (e.g., Stearns 1992; Roff & Fairbairn 2007) might
466 explain the observed concave selection signatures on late fecundity and convex selection on
467 adult survival. Because variation in primate recruitment is already constrained by
468 physiological limitations (Campos *et al.* 2017), when adult survival and recruitment are
469 engaged in a trade-off, this trade-off might lead to our unexpected result. Here, future studies
470 may benefit from deeper insights via cross-second derivatives (Caswell 1996, 2001) to
471 investigate correlations among demographic processes.

472 Examining the drivers of demographic buffering has become an important piece of the
473 ecological and evolutionary puzzle of demography. As such, testing the DBH can help us
474 better predict population responses to environmental variability, climate change, and direct
475 anthropogenic disturbances (Pfister 1998; Boyce *et al.* 2006; McDonald *et al.* 2017; Vázquez *et al.*
476 2017). By setting the DBH into a broader and integrated framework, we hope to enhance
477 comprehension and prediction of the implications of heightened environmental stochasticity
478 on the evolution of life history traits. This understanding is crucial in mitigating the risk of
479 extinction for the most vulnerable species.

480

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487

488 **Data availability**

489 The demographic data used in this paper are open-access and available in the COMPADRE
490 Plant Matrix Database (v. 5.0.1; <https://compadre-db.org/Data/Compadre>). A list of the
491 studies and species used here is available in Supplementary Material (Table S1). If the
492 manuscript is accepted, the data and code supporting the results will be archived on Zenodo.
493 The data and code specific DOI will then be included in our “Data availability” statement.

494

495 **References**

- 496 Barraquand, F. & Yoccoz, N.G. (2013). When can environmental variability benefit population
497 growth? Counterintuitive effects of nonlinearities in vital rates. *Theor Popul Biol*, 89, 1–11.
- 498 Bielby, J., Mace, G.M., Bininda-Emonds, O.R.P., Cardillo, M., Gittleman, J.L., Jones, K.E., *et al.*
499 (2007). The Fast-Slow Continuum in Mammalian Life History: An Empirical Reevaluation. *Am*
500 *Nat*, 169, 748–757.
- 501 Bonsall, M.B. & Klug, H. (2011). The evolution of parental care in stochastic environments. *J Evol*
502 *Biol*, 24, 645–655.
- 503 Boyce, M.S., Haridas, C. V., Lee, C.T., Boggs, C.L., Bruna, E.M., Coulson, T., *et al.* (2006).
504 Demography in an increasingly variable world. *Trends Ecol Evol*, 21, 141–148.
- 505 Brodie, E.I., Moore, A. & Janzen, F. (1995). Visualizing and quantifying natural selection. *Trends*
506 *Ecol Evol*, 10, 313–318.
- 507 Campos, F.A., Morris, W.F., Alberts, S.C., Altmann, J., Brockman, D.K., Cords, M., *et al.* (2017).
508 Does climate variability influence the demography of wild primates? Evidence from long-term
509 life-history data in seven species. *Glob Chang Biol*, 23, 4907–4921.
- 510 Carslake, D., Townley, S. & Hodgson, D.J. (2008). Nonlinearity in eigenvalue-perturbation curves of
511 simulated population projection matrices. *Theor Popul Biol*, 73, 498–505.
- 512 Caswell, H. (1996). Second Derivatives of Population Growth Rate: Calculation and Applications.
513 *Ecology*, 77, 870–879.
- 514 Caswell, H. (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer
515 Associates Inc. Publishers, Sunderland, Massachusetts, USA.

- 516 Charlesworth, B. (1994). *Evolution in age-structured populations*. second edi. Cambridge University
517 Press.
- 518 Le Coeur, C., Yoccoz, N.G., Salguero-Gómez, R. & Vindenes, Y. (2022). Life history adaptations to
519 fluctuating environments: Combined effects of demographic buffering and lability. *Ecol Lett*, 1–
520 13.
- 521 Compagnoni, A., Bibian, A.J., Ochocki, B.M., Rogers, H.S., Schultz, E.L., Sneek, M.E., *et al.* (2016).
522 The effect of demographic correlations on the stochastic population dynamics of perennial
523 plants. *Ecol Monogr*, 86, 480–494.
- 524 Compagnoni, A., Evers, S. & Knight, T. (2023). Spatial replication can best advance our
525 understanding of population responses to climate. *bioRxiv*,
526 <https://doi.org/10.1101/2022.06.24.497542>.
- 527 Doak, D.F., Morris, W.F., Pfister, C., Kendall, B.E. & Bruna, E.M. (2005). Correctly Estimating How
528 Environmental Stochasticity Influences Fitness and Population Growth. *Am Nat*, 166, E14–E21.
- 529 Doak, D.F., Waddle, E., Langendorf, R.E., Louthan, A.M., Isabelle Chardon, N., Dibner, R.R., *et al.*
530 (2021). A critical comparison of integral projection and matrix projection models for
531 demographic analysis. *Ecol Monogr*, 91, e01447.
- 532 Doherty, P.F., Schreiber, E.A., Nichols, J.D., Hines, J.E., Link, W.A., Schenk, G.A., *et al.* (2004).
533 Testing life history predictions in a long-lived seabird: A population matrix approach with
534 improved parameter estimation. *Oikos*, 105, 606–618.
- 535 Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000). Size-Specific Sensitivity: Applying a New
536 Structured Population Model. *Ecology*, 81, 694–708.
- 537 Ellner, S.P., Childs, D.Z. & Rees, M. (2016). Data-driven Modelling of Structured Populations.
- 538 Evans, M.E.K. & Holsinger, K.E. (2012). Estimating covariation between vital rates : A simulation
539 study of connected vs . separate generalized linear mixed models (GLMMs). *Theor Popul Biol*,
540 82, 299–306.
- 541 Ferreira, M., Kajin, M., Vieira, M., Zangrandi, P., Cerqueira, R. & Gentile, R. (2013). Life history of
542 a neotropical marsupial: Evaluating potential contributions of survival and reproduction to
543 population growth rate. *Mamm Biol*, 78, 406–411.
- 544 Franco, M. & Silvertown, J. (2004). A comparative demography of plants based upon elasticities of
545 vital rates. *Ecology*, 85, 531–538.
- 546 Gaillard, J.-M. & Yoccoz, N. (2003). Temporal Variation in Survival of Mammals: a Case of
547 Environmental Canalization? *Ecology*, 84, 3294–3306.
- 548 Gillespie, J.H. (1977). Natural Selection for Variances in Offspring Numbers: A New Evolutionary
549 Principle. *Am Nat*, 111, 1010–1014.
- 550 Griffith, A.B. (2017). Perturbation approaches for integral projection models. *Oikos*, 126, 1675–1686.
- 551 Haridas, C.V. & Tuljapurkar, S. (2005). Elasticities in Variable Environments: Properties and
552 Implications. *Am Nat*, 166, 481–495.
- 553 Healy, K., Ezard, T.H.G., Jones, O.R., Salguero-Gómez, R. & Buckley, Y.M. (2019). Animal life
554 history is shaped by the pace of life and the distribution of age-specific mortality and
555 reproduction. *Nat Ecol Evol*, 3, 1217–1224.

- 556 Heppell, S.S. (1998). Application of Life-History Theory and Population Model Analysis to Turtle
557 Conservation. *Copeia*, 1998, 367.
- 558 Hilde, C.H., Gamelon, M., Sæther, B.-E., Gaillard, J.-M., Yoccoz, N.G. & Pélabon, C. (2020). The
559 Demographic Buffering Hypothesis: Evidence and Challenges. *Trends Ecol Evol*, 35, 523–538.
- 560 Jäkäläniemi, A., Ramula, S. & Tuomi, J. (2013). Variability of important vital rates challenges the
561 demographic buffering hypothesis. *Evol Ecol*, 27, 533–545.
- 562 Jones, J.H. (2007). *Journal of Statistical Software*, 22.
- 563 Jones, J.H. (2011). Primates and the evolution of long, slow life histories. *Current Biology*, 21, R708–
564 R717.
- 565 Jongejans, E., De Kroon, H., Tuljapurkar, S. & Shea, K. (2010). Plant populations track rather than
566 buffer climate fluctuations. *Ecol Lett*, 13, 736–743.
- 567 Koons, D.N., Pavard, S., Baudisch, A. & Jessica E. Metcalf, C. (2009). Is life-history buffering or
568 lability adaptive in stochastic environments? *Oikos*, 118, 972–980.
- 569 Kroon, Hans, D., van Groenendael, J. & Ehrlén, J. (2000). Elasticities: A review of methods and
570 model limitations.
- 571 Lawler, R.R., Caswell, H., Richard, A.F., Ratsirarson, J., Dewar, R.E. & Schwartz, M. (2009).
572 Demography of Verreaux’s sifaka in a stochastic rainfall environment. *Oecologia*, 161, 491–
573 504.
- 574 McDonald, J.L., Franco, M., Townley, S., Ezard, T.H.G., Jelbert, K. & Hodgson, D.J. (2017).
575 Divergent demographic strategies of plants in variable environments. *Nat Ecol Evol*, 1, 0029.
- 576 Morris, W.F., Altmann, J., Brockman, D.K., Cords, M., Fedigan, L.M., Pusey, A.E., *et al.* (2011).
577 Low Demographic Variability in Wild Primate Populations: Fitness Impacts of Variation,
578 Covariation, and Serial Correlation in Vital Rates. *Am Nat*, 177, E14–E28.
- 579 Morris, W.F. & Doak, D.F. (2004). Buffering of Life Histories against Environmental Stochasticity:
580 Accounting for a Spurious Correlation between the Variabilities of Vital Rates and Their
581 Contributions to Fitness. *Am Nat*, 163, 579–590.
- 582 Morris, W.F., Pfister, C.A., Tuljapurkar, S., Haridas, C. V., Boggs, C.L., Boyce, M.S., *et al.* (2008).
583 Longevity can buffer plant and animal populations against changing climatic variability.
584 *Ecology*, 89, 19–25.
- 585 Pélabon, C., Hilde, C.H., Einum, S. & Gamelon, M. (2020). On the use of the coefficient of variation
586 to quantify and compare trait variation. *Evol Lett*, 4, 180–188.
- 587 Pfister, C. (1998). Patterns of variance in stage-structured populations: Evolutionary predictions and
588 ecological implications. *Proceedings of the National Academy of Sciences*, 95, 213–218.
- 589 Reed, A.W. & Slade, N.A. (2012). Buffering and plasticity in vital rates of oldfield rodents. *Journal*
590 *of Animal Ecology*, 81, 953–959.
- 591 Rodríguez-Caro, R.C., Capdevila, P., Graciá, E., Barbosa, J.M., Giménez, A. & Salguero-Gómez, R.
592 (2020). The demographic buffering strategy has a threshold of effectiveness to increases in
593 environmental stochasticity. *bioRxiv*, 1–41.
- 594 Roff, D.A. & Fairbairn, D.J. (2007). The evolution of trade-offs: Where are we? *J Evol Biol*, 20, 433–
595 447.

596 Rotella, J.J., Link, W.A., Chambert, T., Stauffer, G.E. & Garrott, R.A. (2012). Evaluating the
597 demographic buffering hypothesis with vital rates estimated for Weddell seals from 30 years of
598 mark – recapture data, 162–173.

599 Salguero-Gómez, R., Jones, O.R., Archer, C.R., Bein, C., de Buhr, H., Farack, C., *et al.* (2016).
600 COMADRE: A global data base of animal demography. *Journal of Animal Ecology*, 85, 371–
601 384.

602 Shyu, E. & Caswell, H. (2014). Calculating second derivatives of population growth rates for ecology
603 and evolution. *Methods Ecol Evol*, 5, 473–482.

604 Stearns, S. (1992). *The Evolution of Life Histories*. Oxford University Press, New York, USA.

605 Stearns, S.C. (1983). The Influence of Size and Phylogeny on Patterns of Covariation among Life-
606 History Traits in the Mammals. *Oikos*, 41, 173.

607 Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., *et*
608 *al.* (2013). Identification of 100 fundamental ecological questions. *Journal of Ecology*, 101, 58–
609 67.

610 Tuljapurkar, S., Gaillard, J.-M. & Coulson, T. (2009). From stochastic environments to life histories
611 and back. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1499–
612 1509.

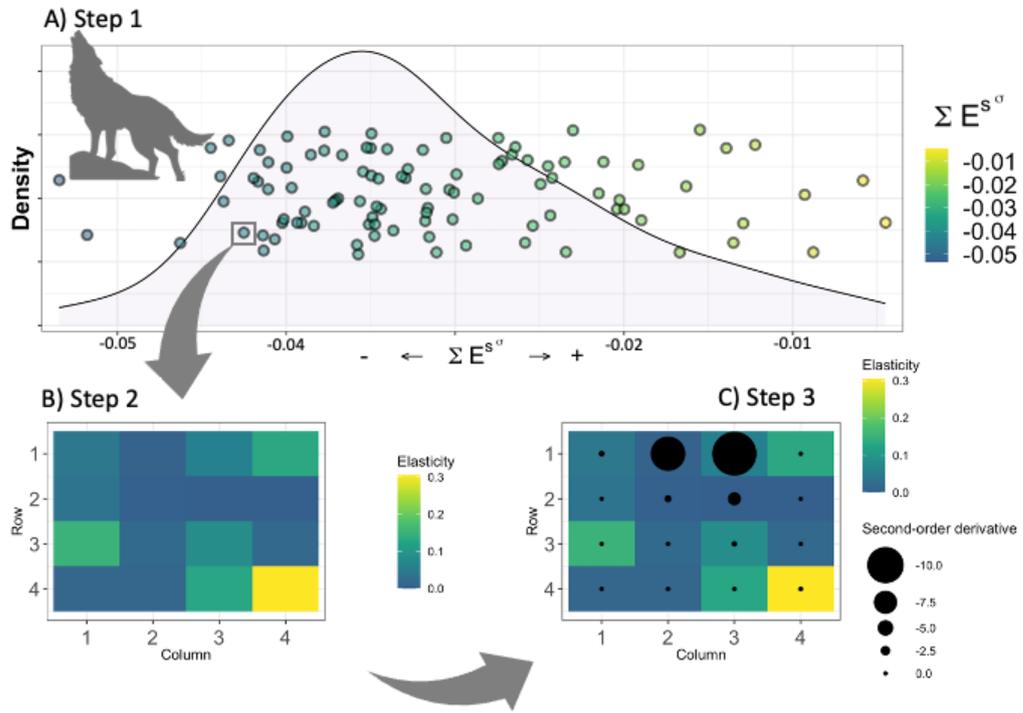
613 Tuljapurkar, S., Horvitz, C.C. & Pascarella, J.B. (2003). The Many Growth Rates and Elasticities of
614 Populations in Random Environments. *Am Nat*, 162, 489–502.

615 Vázquez, D.P., Gianoli, E., Morris, W.F. & Bozinovic, F. (2017). Ecological and evolutionary
616 impacts of changing climatic variability. *Biological Reviews*, 92, 22–42.

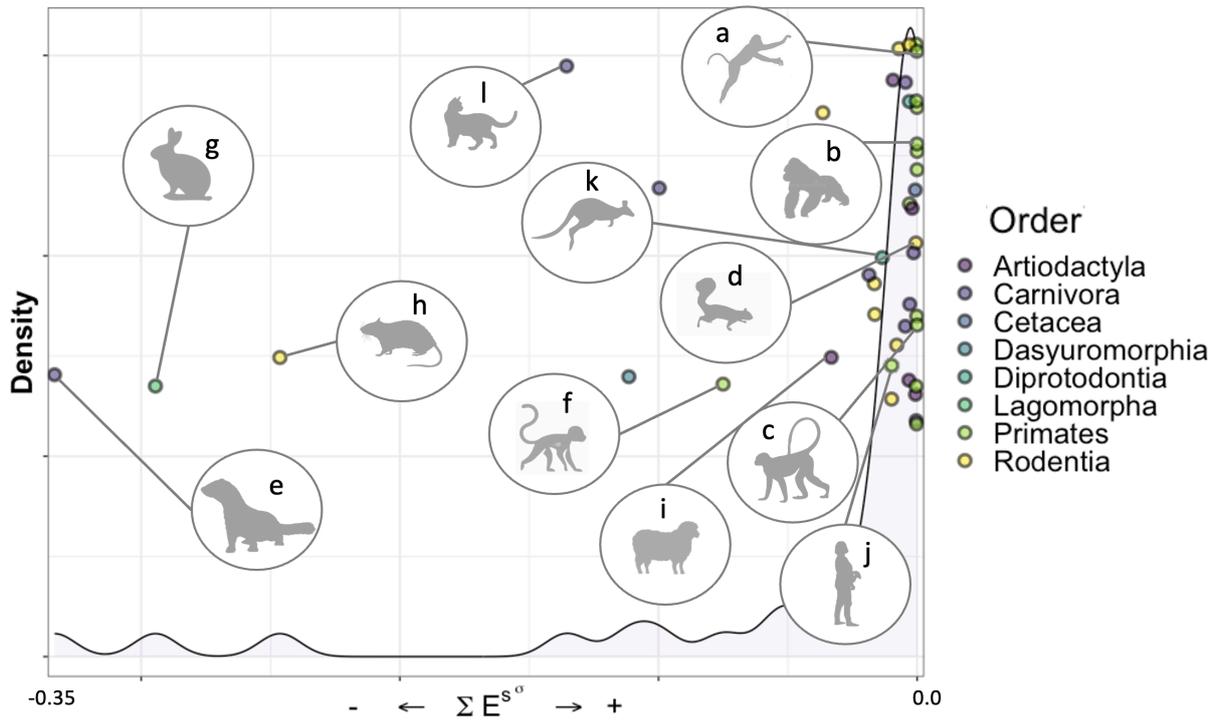
617 Wang, J., Yang, X., Silva Santos, G., Ning, H., Li, T., Zhao, W., *et al.* (2023). Flexible demographic
618 strategies promote the population persistence of a pioneer conifer tree (*Pinus massoniana*) in
619 ecological restoration. *For Ecol Manage*, 529, 120727.

620

621



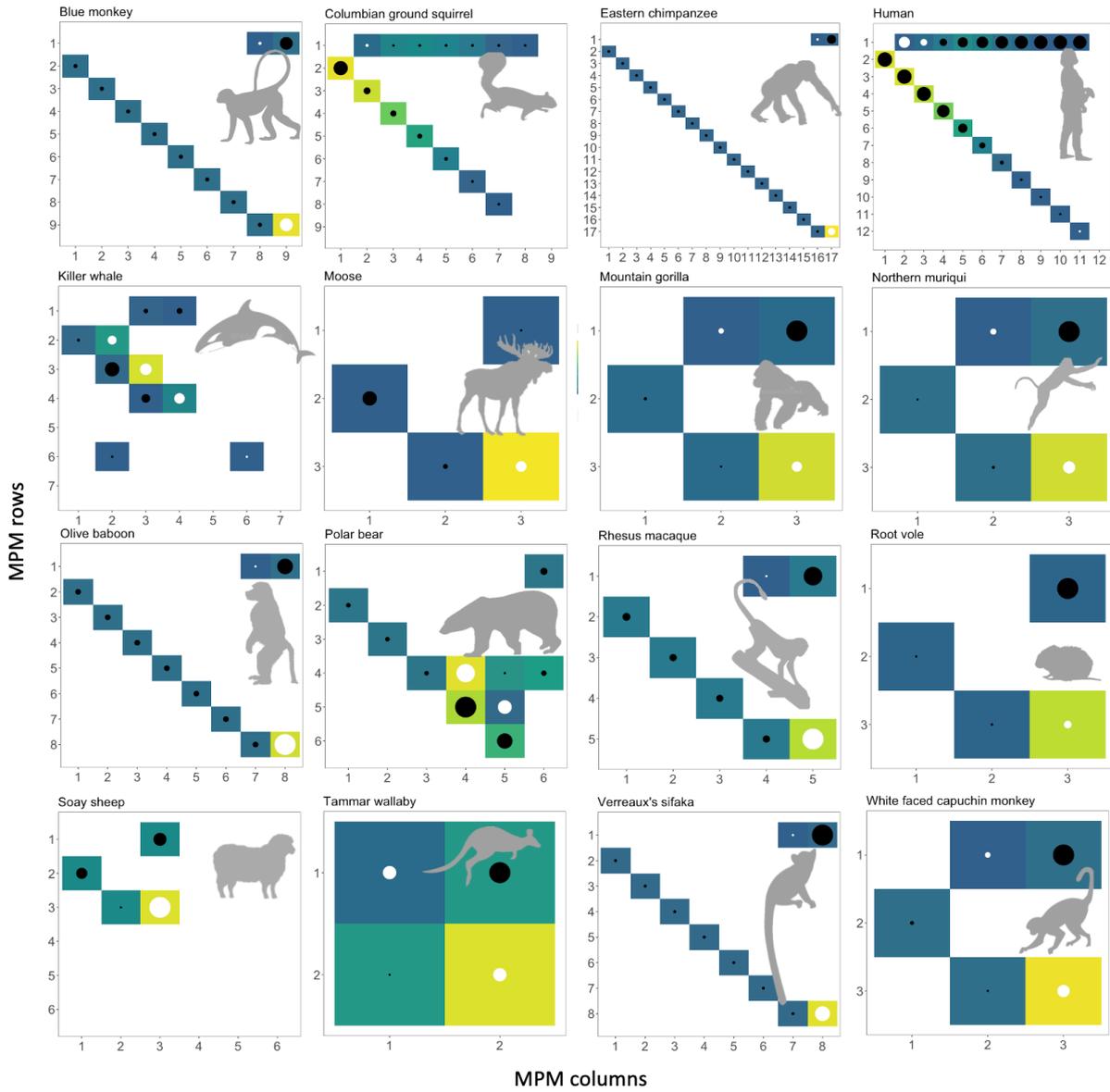
624 **Figure 2**



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627 **Figure 3**



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631 **Figure legends**

632

633 **Figure 1.** A three-step framework proposed to: Step 1 - allocate species and/or populations
634 on a variance continuum (plot A, dots representing 50 hypothetical species). The variance
635 continuum operates at the interspecific level (see text) and is represented by partitioning the
636 sum of all the stochastic elasticities ($\Sigma E_{a_{ij}}^S$) into two compounds: i) sums of stochastic
637 elasticities with respect to the variance ($\Sigma E_{a_{ij}}^{S\sigma}$), and ii) sums of stochastic elasticities with
638 respect to the mean ($\Sigma E_{a_{ij}}^{S\mu}$). The first step of our framework shows the variance compound of
639 the sums of stochastic elasticities forming a continuum where the right-hand side of the plot
640 represents species (or populations) where a perturbation of variance of the most important
641 demographic process results in weak or no impact on λ_s (yellow dots). The yellow-dotted
642 species (or populations) can be classified as having *buffered life-cycles (supporting the DBH)*
643 – based on the most important demographic process for the λ_s . The left-hand side of the graph
644 represents species (or populations) where a perturbation of the variance of the most important
645 demographic process results in strong impact on λ_s (blue dots). Thus, the blue-dotted species
646 (or populations) can be classified as having *unbuffered life cycles (potentially supporting*
647 *DLH, see text)* – based on the most important demographic process for the λ_s . The jitter
648 applied on the y-axis has no biological meaning. Step 2 - Access the linear selection
649 pressures for individual species or populations at intraspecific level (see text) (plot B). Step 2
650 displays the elasticities of the deterministic population growth rate (λ_i) for a hypothetical
651 population of wolf and reveals the linear selection gradients. Step 3 - Access the nonlinear
652 selection pressures at the intraspecific level (see text) (plot C). In the third step self-second
653 derivatives for the corresponding demographic processes from step 2 are displayed.

654

655 **Figure 2.** Results for step 1 of our framework showing the sum of stochastic elasticities with
656 respect to the variance $\Sigma E_{aij}^{S\sigma}$ increase caused by a perturbation in the most relevant
657 demographic process. The 40 populations from 34 species of mammals from the COMADRE
658 database are ranked into the variance continuum from strongly buffered (right-hand side,
659 supporting the DBH) to more variable, less buffered (left-hand side, potentially supporting
660 the DLH, see text). Colors represent different taxonomic orders with Primates occupying the
661 right-hand side. Silhouettes: a) *Brachyteles hypoxantus*, b) *Gorilla beringhei*, c)
662 *Cercopithecus mitis*, d) *Uroditellus columbianus*, e) *Mustela erminea*, f) *Erythrocebus patas*,
663 g) *Lepus americanus*, h) *Rattus fuscipes*, i) *Ovis aries*, j) *Homo sapiens*, k) *Macropus eugenii*,
664 and l) *Felis catus*. The jitter applied on the y-axis has no biological meaning.

665
666 **Figure 3:** Results from steps 2 and 3 of the proposed framework (see Fig. 2B, C). The 16
667 plots represent populations where the MPMs built by ages were available in the COMADRE
668 database (see text). The color scale represents elasticity values for each of the demographic
669 processes in the MPM, where yellow represents high and blue low elasticity values. No color
670 means elasticity=0. Because the aim of step 2 is to identify the most important demographic
671 process within each species' life cycle (the intraspecific level, see text) - not to compare the
672 elasticity values among species - each plot has its own scale (see end of legend). The black
673 dots represent negative self-second derivatives of λ_t - thus concave selection - and the white
674 dots represent positive self-second derivatives of λ_t - thus convex selection. The dot sizes are
675 scaled by the absolute value of self-second derivatives, where the smaller the dot, the closer a
676 self-second derivative is to 0, indicating weak or no selection. Large dots indicate strong
677 selection forces. Scales ($E_{\min-\max}$ =elasticity minimum and maximum value, $SSD_{\min-\max}$ =self-
678 second derivative minimum and maximum value): Blue monkey $E_{\min-\max}=0.00-0.52$, $SSD_{\min-}$
679 $_{\max}=-1.25-1.27$; Columbian ground squirrel: $E_{\min-\max}=0.00-0.23$, $SSD_{\min-\max}=-1.48-0.01$;

680 Eastern chimpanzee: $E_{\min-\max}=0.00-0.60$, $SSD_{\min-\max}=-4.39-2.59$; Human: $E_{\min-\max}=0.00-0.18$,
681 $SSD_{\min-\max}=-0.15-0.08$; Killer whale: $E_{\min-\max}=0.00-0.55$, $SSD_{\min-\max}=-5.72-3.43$; Moose:
682 $E_{\min-\max}=0.00-0.55$, $SSD_{\min-\max}=-0.66-0.36$; Mountain gorilla: $E_{\min-\max}=0.00-0.81$, $SSD_{\min-}$
683 $\max=-1.46-0.28$; Northern muriqui: $E_{\min-\max}=0.00-0.72$, $SSD_{\min-\max}=-1.17-0.35$; Olive baboon:
684 $E_{\min-\max}=0.00-0.54$, $SSD_{\min-\max}=-0.57-1.13$; Polar bear: $E_{\min-\max}=0.00-0.26$, $SSD_{\min-\max}=-$
685 $0.73-0.54$; Rhesus macaque: $E_{\min-\max}=0.00-0.51$, $SSD_{\min-\max}=-0.54-0.71$; Root vole: $E_{\min-}$
686 $\max=0.00-0.86$, $SSD_{\min-\max}=-2.54-0.22$; Soay sheep: $E_{\min-\max}=0.00-0.56$, $SSD_{\min-\max}=-0.22-$
687 0.40 ; Tammar wallaby: $E_{\min-\max}=0.00-0.55$, $SSD_{\min-\max}=-0.64-0.34$; White faced capuchin
688 monkey: $E_{\min-\max}=0.00-0.66$, $SSD_{\min-\max}=-2.66-1.21$.

689

690 **Supplementary material – Data available in COMADRE Version 2.0.1 and results from Step 1 of the framework**

691 **Table S1.** The metadata used in step 1 of our framework and the respective results presented in the main text. The first four columns represent
692 the information from where Matrix Populations Models (MPMs) were extract precisely as presented in COMADRE 2.0.1. Column titles differ
693 from the database as “SpeciesAuthorComadre” is equivalent to “SpeciesAuthor” and “SpeciesName” is equivalent to “SpeciesAccepted” in
694 COMADRE 2.0.1. The remaining columns present the results of step 1, where we present the raw values of $\Sigma E_{aij}^{S\mu}$ and $\Sigma E_{aij}^{S\sigma}$, their respective
695 standard deviation, the stochastic population growth rate λ_s , and the number of available matrices (# matrices). For ByAge, “TRUE” was
696 assigned for MPMs built by age or “FALSE” if otherwise.

SpeciesAuthorComadre	SpeciesName	CommonName	Order	$\Sigma E_{aij}^{S\mu}$	$\Sigma E_{aij}^{S\mu}$ (sd)	$\Sigma E_{aij}^{S\sigma}$	$\Sigma E_{aij}^{S\sigma}$ (sd)	# matrices	λ
Homo_sapiens_subsp_sapiens	<i>Homo sapiens sapiens</i>	Human	Primates	1.003	0.003	1.003	0.004	13	1.064
Alces_alces	<i>Alces alces</i>	Moose	Artiodactyla	1.001	0.001	1.001	0.001	13	1.205
Antechinus_agilis	<i>Antechinus agilis</i>	Agile antechinus	Dasyuromorphia	1.111	0.111	1.111	0.011	2	0.931
Brachyteles_hypoxanthus	<i>Brachyteles hypoxanthus</i>	Northern muriqui	Primates	1.000	0.000	1.000	0.000	12	1.051
Callospermophilus_lateralis	<i>Callospermophilus lateralis</i>	Golden-mantled ground squirrel	Rodentia	1.054	0.054	1.054	0.055	9	2.052
Cebus_capucinus	<i>Cebus capucinus</i>	White faced capuchin monkey	Primates	1.000	0.000	1.000	0.000	11	1.021
Cercopithecus_mitis	<i>Cercopithecus mitis</i>	Blue monkey	Primates	1.000	0.000	1.000	0.000	14	1.036
Eumetopias_jubatus	<i>Eumetopias jubatus</i>	Northern sea lion; Steller sea lion	Carnivora	1.005	0.005	1.005	0.002	2	0.904
Felis_catus	<i>Felis catus</i>	Feral cat	Carnivora	1.136	0.136	1.136	0.012	1	1.948
Gorilla_beringei	<i>Gorilla beringei</i>	Mountain gorilla	Primates	1.000	0.000	1.000	0.000	21	1.027
Hippocamelus_bisulcus	<i>Hippocamelus bisulcus</i>	Huemul deer	Artiodactyla	1.002	0.002	1.002	0.001	1	0.996
Lepus_americanus	<i>Lepus americanus</i>	Snowshoe hare	Lagomorpha	1.294	0.294	1.294	0.165	2	0.812
Lycaon_pictus	<i>Lycaon pictus</i>	African wild dog	Carnivora	1.100	0.100	1.100	0.008	1	1.500
Macaca_mulatta_3	<i>Macaca mulatta</i>	Rhesus macaque	Primates	1.000	0.000	1.000	0.001	12	1.127
Macropus_eugenii	<i>Macropus eugenii</i>	Tammar wallaby	Diprotodontia	1.013	0.013	1.013	0.012	7	0.981

Marmota_flaviventris_2	<i>Marmota flaviventris</i>	Yellow-bellied marmot	Rodentia	1.007	0.007	1.007	0.006	4	0.890
Marmota_flaviventris_3	<i>Marmota flaviventris</i>	Yellow-bellied marmot	Rodentia	1.008	0.008	1.008	0.005	4	0.921
Microtus_oeconomus	<i>Microtus oeconomus</i>	Root vole	Rodentia	1.000	0.000	1.000	0.001	14	1.028
Mustela_erminea	<i>Mustela erminea</i>	Stoat	Carnivora	1.334	0.334	1.334	0.117	2	1.258
Orcinus_orca_2	<i>Orcinus orca</i>	Killer whale	Cetacea	1.001	0.001	1.001	0.001	24	0.999
Ovis_aries_2	<i>Ovis aries</i>	Soay sheep	Artiodactyla	1.033	0.033	1.033	0.020	3	1.099
Pan_troglodytes_subsp._schweinfurthii	<i>Pan troglodytes</i>	Eastern chimpanzee	Primates	1.000	0.000	1.000	0.001	22	0.982
Papio_cynocephalus	<i>Papio cynocephalus</i>	Olive baboon	Primates	1.000	0.000	1.000	0.000	19	1.054
Peromyscus_maniculatus_2	<i>Peromyscus maniculatus</i>	Deer mouse	Rodentia	1.010	0.010	1.010	0.005	2	1.107
Phocarcetos_hookeri	<i>Phocarcetos hookeri</i>	New Zealand sea lion	Carnivora	1.005	0.005	1.005	0.003	8	1.023
Propithecus_verreauxi	<i>Propithecus verreauxi</i>	Verreaux's sifaka	Primates	1.000	0.000	1.000	0.000	12	0.986
Puma_concolor_8	<i>Puma concolor</i>	Cougar	Carnivora	NA	NA	NA	NA	10	1.115
Rattus_fuscipes	<i>Rattus fuscipes</i>	Bush rat	Rodentia	1.246	0.246	1.246	0.029	2	1.305
Spermophilus_armatus	<i>Urocitellus armatus</i>	Uinta ground squirrel	Rodentia	1.016	0.016	1.016	0.011	4	1.125
Spermophilus_armatus_2	<i>Urocitellus armatus</i>	Uinta ground squirrel	Rodentia	1.017	0.017	1.017	0.010	3	1.095
Spermophilus_columbianus	<i>Urocitellus columbianus</i>	Columbian ground squirrel	Rodentia	1.036	0.036	1.036	0.025	3	1.009
Spermophilus_columbianus_3	<i>Urocitellus columbianus</i>	Columbian ground squirrel	Rodentia	1.003	0.003	1.003	0.006	3	1.200
Ursus_americanus_subsp._floridanus	<i>Ursus americanus</i>	Florida black bear	Carnivora	1.003	0.003	1.003	0.003	2	1.020
Ursus_arctos_subsp._horribilis_5	<i>Ursus arctos</i>	Grizzly bear	Carnivora	1.001	0.001	1.001	0.001	4	1.026
Ursus_maritimus_2	<i>Ursus maritimus</i>	Polar bear	Carnivora	1.019	0.019	1.019	0.007	2	0.941
Brachyteles_hypoxanthus_2	<i>Brachyteles hypoxanthus</i>	Northern muriqui	Primates	1.000	0.000	1.000	0.000	12	1.111
Cebus_capucinus_2	<i>Cebus capucinus</i>	WhiteNAfaced capuchin monkey	Primates	1.000	0.000	1.000	0.000	11	1.059
Chlorocebus_aethiops_2	<i>Chlorocebus aethiops</i>	Vervet	Primates	1.075	0.075	1.075	0.087	5	1.187
Erythrocebus_patas	<i>Erythrocebus patas</i>	Patas monkey	Primates	1.051	0.051	1.051	0.038	5	1.128
Gorilla_beringei_subsp._beringei	<i>Gorilla beringei</i>	Mountain gorilla	Primates	1.000	0.000	1.000	0.000	21	1.053

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