To buffer or to be labile? A framework to disentangle demographic patterns and evolutionary processes

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17 **Abstract**

18 Until recently, natural selection was assumed to reduce temporal fluctuation in vital
 19 rates due to its negative effects on population dynamics – the so-called Demographic
 20 Buffering Hypothesis (DBH). After several failures to support the DBH in the two
 21 decades since it was first posited, an alternative hypothesis was suggested; the
 22 Demographic Lability Hypothesis (DLH), where population vital rates should track
 23 rather than buffer the environmental conditions. Despite the huge contribution of both
 24 hypotheses to comprehend the demographic strategies to cope the environmental
 25 stochasticity, it remains unclear if they represent two competing patterns or the extreme
 26 ends of a continuum encompassing all demographic strategies. To solve this historical
 27 debate, we unify several methods with an integrative theoretical approach where: i)
 28 using the sum of stochastic elasticity with respect to mean and variance – a first-order
 29 derivative approach – we rank species on a Buffering-Lability (DB-DL) continuum and
 30 ii) using the second-order derivative, we examine how vital rates are shaped by natural
 31 selection. Our framework, applied to 40 populations of 34 mammals, successfully
 32 placed the species on the DB-DL continuum. We could also link the species' position
 33 on the DB-DL continuum to their generation time and time to recovery. Moreover, the
 34 second-order derivative unveiled that vital rates with lower temporal variation are not
 35 necessarily under a strong pressure of stabilizing selection, as predicted by DBH and
 36 DLH. Our framework provides an important step towards unifying the different
 37 perspectives of DBH and DLH with key evolutionary concepts.

38

39 **Keywords:** COMADRE Animal Matrix Database, elasticity, life-history evolution,
 40 second-order derivative, sensitivity, vital rate variance.

41 **Introduction**

42 Modern demographic theory offers a wide array of hypotheses to explain the
 43 evolutionary processes that shape the diversity of demographic responses to
 44 environmental stochasticity (Charlesworth 1994, Pfister 1998, Healy *et al.* 2019, Hilde
 45 *et al.* 2020). Of these, two stand out as the most promising in linking evolutionary
 46 processes to demographic patterns: the Demographic Buffering Hypothesis (DBH) and
 47 its alternative hypothesis, the Demographic Lability Hypothesis (DLH) (Koons *et al.*
 48 2009, Jongejans *et al.* 2010, McDonald *et al.* 2017, Hilde *et al.* 2020). Together, the
 49 DBH and DLH (hereafter *DB-DL perspective*), represent two contrasting ways by which
 50 natural populations cope with environmental stochasticity by either buffering (DBH) or
 51 tracking (DLH) changes in environmental conditions (Morris *et al.* 2008, McDonald *et*
 52 *al.* 2017, Hilde *et al.* 2020).

53 Coined over two decades ago, the DBH postulates that vital rates (*e.g.* survival,
 54 fecundity) that have the greatest influence on population growth should buffer the
 55 negative effects of the environmental stochasticity by presenting lower temporal
 56 variation than less influential vital rates (Pfister 1998). Because local extinction risk
 57 typically increases with increasing fluctuations in population size (Ovaskainen and
 58 Meerson 2010), demographic buffering is hypothesized to be a result of natural
 59 selection. This evolutionary process reducing variation in vital rates, called
 60 environmental canalization (Debat and David 2001, Gaillard and Yoccoz 2003), is
 61 expected to be more intense in vital rates that contribute the most to population growth
 62 rate (Pfister 1998).

63 Demographic buffering is expected to be particularly important for species that
 64 are less capable to recover after perturbations, which have also a higher risk of
 65 extinction due to demographic stochasticity (*e.g.* long-lived trees and primates, Morris

66 *et al.* 2008, 2011, Hilde *et al.* 2020). Contrastingly, the DLH postulates that some
67 species might take advantage if their vital rates were labile enough to permit population
68 size track rather than buffering the environmental stochasticity (Koons *et al.* 2009,
69 2014, Jongejans *et al.* 2010, Hilde *et al.* 2020).

70 The DB-DL perspective simultaneously reflects *demographic patterns*, *i.e.* how
71 populations respond to the environmental stochasticity (Morris *et al.* 2008, Jongejans *et*
72 *al.* 2010, McDonald *et al.* 2017), and *evolutionary processes*, *i.e.* how the life-histories
73 of the individuals that make up those populations were shaped by natural selection
74 (Pfister 1998, Gaillard and Yoccoz 2003, Koons *et al.* 2009). Both demographic and
75 evolutionary facets are important to predict the eco-evolutionary dynamic in response to
76 climate changes (Metcalf and Pavard 2007, Burns *et al.* 2010, Salguero-Gómez *et al.*
77 2018). Despite the importance of understanding demographic responses to
78 environmental changes, existing approaches to assess the DBH and DLH present
79 several constraints and can therefore hinder our understanding of the eco-evolutionary
80 processes behind the DB-DL perspective (Box 1, 2).

81 After two decades of consolidating the methodological bases of the DB-DL
82 perspective (Hilde *et al.* 2020), a lack of consensus on how to identify evidence in favor
83 of the DBH and DLH still persists (Box 1). Moreover, the bases of the DBH and DLH
84 have been mainly developed in terms of mathematical models rather than trait-based
85 mechanisms (Hilde *et al.* 2020). Indeed, only few authors have suggested trait-based
86 mechanisms to support the DB-DL perspective (Morris *et al.* 2008, McDonald *et al.*
87 2017). Of those, even the prevalence of DBH in long-lived species is not well supported
88 (Morris *et al.* 2011, Reed and Slade 2012, McDonald *et al.* 2017). Additionally, other
89 attempts have found no correlation between the DBH and DLH and other life-history

90 traits (*e.g.* generation time), environmental variables, nor phylogenetic relationships
91 (McDonald *et al.* 2017).

92 In this study, we show that the lack of patterns in the assessment of DBH and
93 DLH arises from different interpretations of what the two main approaches to assess
94 them consider as evidence for DBH and DLH. Here we will refer to these approaches as
95 multi-species comparative approaches (*e.g.* Morris *et al.* 2008, McDonald *et al.* 2017)
96 and (very often single population) hypothesis testing approaches (*e.g.* Reed and Slade
97 2012, Jäkäläniemi *et al.* 2013). We argue that these approaches represent two
98 perspectives with very distinctive eco-evolutionary implications that should be
99 disentangled to better understand the performance and the evolutionary processes of the
100 buffering and lability demographic strategies. To better assess the multiple facets of the
101 DB-DL perspective, we reconcile different methods developed over the last two decades
102 in a unified framework. Finally, we demonstrate the insights provided by our
103 framework to better understand how species and populations both respond to and are
104 shaped by environmental stochasticity.

Box 1. Standard protocol to assess the DBH and DLH

The usage of simple correlation analyses (particularly the Spearman's correlation) has been the most frequent approach to assess the DBH and DLH ever since they were posited (Pfister 1998, Hilde *et al.* 2020). Yet, two competing interpretations exist regarding the outcome of such correlation analyses (below). The lack of agreement between the two interpretations highlights the lack of consensus on how the demographic buffering vs. lability strategies manifest themselves in life histories.

The two competing interpretations of the correlation analyses to assess the DBH and DLH are based on different perspectives. Some researchers are interested in unveiling the patterns and distribution of the two demographic strategies - DBH and DLH across the tree of life in a multi-species comparative approaches (Jongejans *et al.* 2010, McDonald *et al.* 2017). Contrastingly, other researchers who assess DBH and DLH in terms of hypothesis testing are interested in finding support for one of these hypotheses by examining how natural selection have shaped the variance in vital rates (Reed and Slade 2012, Rotella *et al.* 2012). While the hypothesis testing approach looks for evidence to corroborate the patterns expected by either DBH or DLH (*e.g.* Jäkäläniemi *et al.* 2013), the multi-species comparative approaches assumes that all demographic strategies should lie somewhere between completely buffered (DBH) and completely labile (DLH)(*e.g.* McDonald *et al.* 2017). However, despite the well documented evidence in favor of the DBH, only scarce evidence exists to support the DLH (Hilde *et al.* 2020). Furthermore, the quantitative assessment of DBH and DLH reflects these different views of the comparative and hypothesis testing approaches as we show below.

Consider the example in Fig 1, where a negative Spearman's correlation coefficient of -0.45 with $P > 0.05$ is shown. Despite the non-significant results, patterns

like this have been used as evidence of demographic buffering in the multi-species comparative approaches (e.g. Doak *et al.* 2005, McDonald *et al.* 2017). Thus, the correlation coefficient is used as an index to place populations into the continuum, ranging from completely demographically buffered (Spearman's correlation $\rho = -1$) to completely demographically labile ($\rho = 1$), regardless of the P-value (McDonald *et al.* 2017) - hereafter, *Demographic buffering-lability continuum* (or *DB-DL continuum*). However, other authors interpret the absence of statistical support for the DBH as evidence in favor of the DLH (e.g. Jäkäläniemi *et al.* 2013) or the absence of any particular strategy, neither DBH nor DLH (e.g. Reed and Slade 2012).

Figure 1. A hypothetical Matrix Population Model comparing the temporal variation in each matrix element. Letters represent (st-)age transitions (growth, stasis, and shrinkage – t) and recruitment (r), and the subscripts in the matrix element a_{ij} correspond to transitions or recruitment events from stage j (column in matrix A) in time t , to state i (row in A) in $t+1$. The solid line represents the linear trend calculated by the least squares regression. The Spearman's correlation coefficient (ρ) between the two variables and its P-value are informed in the figure.

147 **Disentangling demographic patterns and evolutionary processes in the DB-DL** 148 **perspective: buffering mechanisms vs. canalization of variance**

149 All populations are buffered in someway (Hunter 2009). Thus, the major
150 question is not *if* but *to what extent* the populations are dependent on environmental
151 stochasticity. Some traits, like endothermy or migration, can help individuals to buffer
152 (or avoid) the negative effects of environmental conditions (Fuller *et al.* 2010, Edic *et*
153 *al.* 2020). On the another hand, traits like fixed litter size and long parental care may be
154 buffered, once they remain constant independently of environmental conditions (Meiri
155 *et al.* 2020, Santos *et al. in prep*). All these traits which increase the capacity of an
156 individual to buffer the effects of environmental stochasticity may be considered as
157 buffering mechanisms (Santos *et al. in prep*). Ultimately, the capacity of the species to
158 buffer the environmental stochasticity should be proportional to the set of buffering
159 mechanisms of these species - including those traits which limit the population to
160 increase in the good years (*e.g.* bonanzas).

161 Some patterns are expected to arise from these multiple traits. For example,
162 bigger, long-lived species should be more buffered than smaller, shorter-lived species
163 (Morris *et al.* 2008). Yet, such patterns do not tell us how these buffering traits have
164 been shaped by natural selection (*i.e.* what processes led to these patterns). To assess the
165 processes which underly these patterns, we need to analyze the *force and direction of*
166 *natural selection acting on them*. Thus, if the temporal variation in an important
167 buffering trait (*e.g.* longevity, age of first reproduction) exerts a negative impact on
168 individual performance, its temporal variation might be canalized - *i.e. stabilizing*
169 *selection* (Debat and David 2001) - increasing the population's capacity to buffer the
170 environmental stochasticity. Otherwise, natural selection might promote variation in the

171 expression of these traits if they improve the individual performance in a variable
172 environment, *i.e. disruptive selection* (Pasztor *et al.* 2000, Koons *et al.* 2009, 2014).

173 **A unified framework to assess the multiple facets of the DBH and DLH**

174 Here, we propose a framework that overcomes the limitations of previous
175 approaches (Box 1, 2) by explicitly disentangling demographic patterns from the
176 evolutionary processes shaping the different vital rates. The application of this
177 framework requires three steps which include two additional steps to the most largely
178 used approaches to quantify DBH vs. DLH: the correlative analyses (Box 1). The **step 1**
179 in the framework consists of comparing to what extent the life histories are variable and
180 rank the populations of multiple species according to whether they are buffered or
181 environmental dependent (labile) (Fig. 2A). **Step 2** and **step 3** are focused on
182 populations rather than species. The **step 2** is analogous to the correlative analyses.
183 However, we limited this step to visual inspection of biplots representing the relation
184 between the temporal variance of vital rates and their contribution to population growth
185 rate for each population. The graphical inspection of biplots helps to make inferences
186 about the forces of natural selection acting on each vital rate before the empirical
187 assessment by step 3. Finally, **step 3** enables to assess how temporal variance in
188 survival and reproduction are shaped by natural selection (Figs. 2 B, C).

189 Our unified framework provides a link between the DBH and DLH to
190 evolutionary mechanisms, *i.e.* disruptive and stabilizing selection, where natural
191 selection acts to reduce or increase the temporal variance in a specific vital rate (Fig.
192 2C). The full approach of our framework is explained in detail below, after a concise
193 description of structured population models (in terms of both matrix population models
194 [MPM hereafter; Caswell 2001] and integral projection models [IPM hereafter; Ellner *et*

195 *al.* 2016]) - the common tools to assess the relative contribution of vital rates to
196 population growth rate (de Kroon *et al.* 1986, Pfister 1998, Hilde *et al.* 2020).

197

198 *The mathematical bases of the framework*

199 The DBH and DLH have been mainly assessed by MPM (*e.g.* Pfister 1998,
200 Rotella *et al.* 2012) and IPM (*e.g.* Rodríguez-Caro *et al.* 2020), which represent the
201 analytical foundation for our framework. Both MPMs and IPMs are stage-structured,
202 discrete-time demographic models (Caswell 2001, Ellner *et al.* 2016). In both,
203 individuals in a population are categorized according to discrete (*e.g.* age, stage, as in
204 MPMs; Caswell 2001) or continuous traits (*e.g.* size, height, as in IPMs; Easterling *et*
205 *al.* 2000). For simplicity, for the rest of the framework description we focus on the
206 usage of MPMs, but note that the same approaches are applicable to IPMs (*e.g.* Griffith
207 2017).

208 MPMs are matrix representations of life cycles (Ebert 1999). In an MPM $\mathbf{A}$,
209 each element a_{ij} represents a demographic process, for example, a transition from a (st-
210)age to another or a contribution of a given (st-)age to the recruitment of new
211 individuals. It is well known that each demographic process, a_{ij} , contributes differently
212 to the population growth rate (λ) depending on the life cycle and life history of the
213 species (Silvertown *et al.* 1993). This contribution of a_{ij} to λ , named *sensitivity*, can be
214 assessed by simulating small changes on a_{ij} or by the partial first-order derivative of
215 each element in the matrix $\mathbf{A}$ with respect to λ (Caswell 2001, Tuljapurkar *et al.* 2003).
216 As the sensitivities are dependent on the initial values of a_{ij} , they are not comparable as
217 some represent survival (bounded from 0-1) while others represent recruitment (≥ 0).
218 Thus, to compare sensitivities for survival and recruitment, they must be rescaled to
219 proportional contributions to λ , the so-called *elasticities* e_{ij} (Caswell 2001).

220 As survival and recruitment are always, in some way, dependent on the current
 221 environmental conditions (Hunter 2009), we must expect (1) different values of a_{ij} for
 222 each time t sampled and (2) a different population growth rate for each time t , λ_t
 223 (Tuljapurkar *et al.* 2003). Moreover, in a stochastic environment, stochastic population
 224 growth rate (λ_s) is a multiplicative process of bad and good years for the population
 225 (Morris and Doak 2002). Due to the multiplicative process that characterizes the λ_s , the
 226 arithmetic mean of multiples λ_t ($\bar{\lambda}$) is not equivalent to λ_s because the temporal
 227 dependence of λ_s was not accounted for in $\bar{\lambda}$ (Tuljapurkar *et al.* 2003). Indeed, very
 228 often $\lambda_s < \bar{\lambda}_t$ (Morris and Doak 2002). Additionally, elasticity in a stochastic
 229 perspective, namely stochastic elasticity, e_{ij}^s , is composed of its mean and its variance,
 230 which both contribute to the stochastic population growth rate λ_s (Tuljapurkar *et al.*
 231 2003). Integrating these stochastic elasticities allow us to assess the effect of variation
 232 in each vital rate weighted by its relative contribution to λ_s as explained below.

233

234 *Comparing different life history responses to the environmental conditions*

235 The sum of all stochastic elasticities ($\Sigma E_{a_{ij}}^s$) of an MPM $\mathbf{A}$ must be equal to 1
 236 because it represents the contribution of all elements a_{ij} to the stochastic population
 237 growth rate (λ_s) (Tuljapurkar *et al.* 2003, Haridas and Tuljapurkar 2005). Moreover the
 238 sum of all stochastic elasticities ($\Sigma E_{a_{ij}}^s$) can be decomposed to assess how temporal
 239 variance and mean values of each vital rates contribute to λ_s – they are respectively the
 240 *sum of stochastic elasticity with respect of the variance* $\Sigma E_{a_{ij}}^{s\sigma}$, and the *sum of stochastic*
 241 *elasticity with respect of the mean* $\Sigma E_{a_{ij}}^{s\mu}$. Once again, $\Sigma E_{a_{ij}}^{s\sigma} + \Sigma E_{a_{ij}}^{s\mu}$ should be equal to
 242 1 because $\Sigma E_{a_{ij}}^s = \Sigma E_{a_{ij}}^{s\sigma} + \Sigma E_{a_{ij}}^{s\mu}$.

243 The $\Sigma E_{a_{ij}}^{S^{\sigma}}$, if applied to MPMs, might range from 0 to -1, producing a continuum
 244 of species' responses that is similar to the predictions provided by the DBH and DLH
 245 (Box 1) – the *DB-DL* continuum (Haridas and Tuljapurkar 2005, Morris *et al.* 2008). A
 246 population with $\Sigma E_{a_{ij}}^{S^{\sigma}}$ close to 0 - the *Demographic Buffered-end* (or *DB-end*) - has only
 247 a minor temporal variation in its vital rates, particularly in those vital rates that have a
 248 major contribution to λ_s . The higher the variance in the most important vital rates, the
 249 further the population will be from $\Sigma E_{a_{ij}}^{S^{\sigma}} = 0$ (Fig. 2A). In other words, the further a
 250 population is from $\Sigma E_{a_{ij}}^{S^{\sigma}} = 0$, the closer it is to the *DL-end* of the DB-DL continuum.
 251 As the $\Sigma E_{a_{ij}}^S = \Sigma E_{a_{ij}}^{S^{\sigma}} + \Sigma E_{a_{ij}}^{S^{\mu}}$, any change in $\Sigma E_{a_{ij}}^{S^{\sigma}}$ will reflect in $\Sigma E_{a_{ij}}^{S^{\mu}}$, thus, both
 252 values will provide the same information.

253 The values of $\Sigma E_{a_{ij}}^{S^{\sigma}}$ and $\Sigma E_{a_{ij}}^{S^{\mu}}$ represent how species responded to the
 254 environmental stochasticity during the time sampled (Tuljapurkar *et al.* 2003). These
 255 values should vary from population to population according to the environmental
 256 conditions which populations were exposed to at the time, thus, the $\Sigma E_{a_{ij}}^{S^{\sigma}}$ and $\Sigma E_{a_{ij}}^{S^{\mu}}$
 257 have also been referred as *the relative effect of environmental variation to population*
 258 *growth rate* (Morris *et al.* 2008). Yet, the $\Sigma E_{a_{ij}}^{S^{\sigma}}$ and $\Sigma E_{a_{ij}}^{S^{\mu}}$ should vary according to
 259 species-specific range, because there are limits to how the most important vital rates can
 260 vary without the population becoming extinct, particularly regarding survival (*e.g.*
 261 Rodríguez-Caro *et al.* 2020). We also expect limits on reproductive output imposed by
 262 physiology and morphology of some species (*e.g.* Meiri *et al.* 2020). Ultimately, both
 263 $\Sigma E_{a_{ij}}^{S^{\sigma}}$ and $\Sigma E_{a_{ij}}^{S^{\mu}}$ and the coefficient of correlation, can be used to place populations in a
 264 DB-DL continuum (Box 1). However, unlike previous methods, the $\Sigma E_{a_{ij}}^{S^{\sigma}}$ and $\Sigma E_{a_{ij}}^{S^{\mu}}$
 265 overcomes the key limitations characteristic of the correlative analyses and allows
 266 assessing DBH and DLH evidence more clearly (Box 2).

267 *Revealing the evolutionary processes that shape the life histories*

268 Evolutionary processes have been immediately evoked to explain the patterns
269 arising from the comparative approach when assessing the position of species along the
270 DB-DL continuum (Morris *et al.* 2011, McDonald *et al.* 2017). Thus, species placed at
271 the DB-end of the continuum are commonly expected to be under strong selection
272 pressures to reduce temporal variation in their most important vital rates (Gaillard and
273 Yoccoz 2003). Contrastingly, natural selection is claimed to promote temporal variation
274 in the most important vital rates in those species placed at DL-end of the continuum
275 (Koons *et al.* 2009, 2014). Such evolutionary claims behind the DB-DL continuum are
276 key to bridge the gap between demographic and evolutionary processes but remain
277 unsupported by previous studies which failed to find consistent patterns (McDonald *et*
278 *al.* 2017). To test these predictions, we use the evolutionary assumptions of stage-
279 structured population models and their mathematical proprieties, as detailed below.
280 Again, we focus on MPMs, but the same properties also emerge from IPMs (Ellner *et*
281 *al.* 2016).

282 Matrix Population Models have been used numerous times to identify the
283 evolutionary processes at the population level (*e.g.* Lande 1982, Coulson *et al.* 2006, de
284 Vries *et al.* 2020). Because the mean values of the matrix elements a_{ij} represent the
285 mean performance of individuals at each (st-)age in surviving and transmitting their
286 genes to the next generation, the population growth rate assessed by the MPM (λ) is
287 assumed to be a proxy for the mean fitness of a population (Lande 1982, Brodie *et al.*
288 1995, Coulson *et al.* 2006, Metcalf and Pavard 2007, Engen *et al.* 2011). If λ can be
289 used as a proxy for the mean fitness, each a_{ij} is one of the fitness components and its
290 contribution to the mean fitness can be quantified with its respective *sensitivity*.
291 Nevertheless, the sensitivity obtained as the first-order derivative of a_{ij} , assumes a

linear relationship between a demographic process a_{ij} and λ , even though this assumption is often violated in natural systems (Caswell 1996). The non-linearity between the contribution of each a_{ij} and λ is adequately verified (and quantified) by using the second-order derivatives of pairs of a_{ij} (Caswell 1996).

The assumption that λ_s is approximately the long-term mean fitness in a population in a stochastic environment (*e.g.* Lande 1982, Coulson *et al.* 2006, de Vries *et al.* 2020), allows us to interpret the results from second-order derivative in terms of disruptive and stabilizing selection (Caswell 1996, McCarthy *et al.* 2008, Shyu and Caswell 2014). Therefore, if the second-order derivative of demographic process a_{ij} is negative – representing a concave function ($\cap$ -shaped) - natural selection tends to reduce temporal variation in a_{ij} (Brodie *et al.* 1995). We can expect a negative second-order derivative for demographic processes a_{ij} with high contribution to fitness and low temporal variance, evidencing buffering as well as an environmental canalization process – a prediction from the DBH (Pfister 1998, Gaillard and Yoccoz 2003). On the other hand, if the second-order derivative is positive (U-shaped), the temporal variance of demographic process should increase, thus evidencing a disruptive selection, as predicted by the DLH (Pasztor *et al.* 2000, Koons *et al.* 2009, 2014).

311

312 Figure 2. A unified framework placing life histories along a continuum of demographic
313 buffering vs. demographic lability and linking the demographic processes to the
314 underlying key evolutionary processes. Arrows show the flow between each step. Step 1
315 allocates (rank) each life history into the DB-DL continuum using the $\Sigma E_{a_{ij}}^{\mu}$ and $\Sigma E_{a_{ij}}^{\sigma}$.
316 This step produces a diagonal line where species are placed according to their responses
317 to environmental stochasticity, from the more buffered on the top left corner, to more
318 labile on the bottom right corner. A population will move along the diagonal continuum,
319 from the top left towards the bottom right corner, if its demographic processes a_{ij} vary
320 more across time – particularly the most contributive a_{ij} . Dots represent 50 hypothetical
321 life histories and colors represent the relative place along the continuum from more
322 buffered (blue) to more labile (red). To perform steps 2 and 3, we must look at each
323 population (each dot) in step 1, separately. Here we represent a hypothetical population
324 from a hypothetical wolf species to assess whether the evolutionary process acting on its
325 vital rates or demographic processes (or a_{ij} for MPMs) correspond to expectations posit
326 by the DBH and DLH. In step 2, we plot the elasticity of each vital rate or demographic
327 process, a_{ij} , vs. its coefficient of temporal variation providing a visual guide to evaluate

328 the trend between temporal variance and its contribution to λ . Note that this step is
 329 common with most approaches that assess DBH and DLH, but, in our framework, it
 330 only serves to visually inspect the relationship. Finally, step 3 quantifies the type of
 331 natural selection driving the temporal variation in each demographic process, by
 332 obtaining the second-order derivatives, represented by different colors – from
 333 stabilizing selection (second-order derivatives < 0) in blue to disruptive selection
 334 (second-order derivatives > 0) in red.

335

336

337 **Box 2. Advantages of the unified analytical framework**

338 Numerous limitations in using correlative analyses to assess the DBH and DLH
339 have been pointed out since it was first proposed by Pfister (1998) (Morris and Doak
340 2004, Doak et al. 2005, McDonald et al. 2017). While some of these limitations have
341 been overcome with corrective methods, others remain neglected. Below, we point out
342 these limitations and how the framework proposed to handle them in contrast to the
343 correlative analyses – the dominant approach to assess DBH and DLH (Table 1).

344 **Mean-variance scale:** Different demographic processes cannot be compared
345 because they have different magnitudes of mean and variance (Morris and Doak 2004).
346 For instance, consider two survival rates s_1 ($\bar{x} = 0.6 \pm 0.1$) and s_2 ($\bar{x} = 0.9 \pm 0.1$). Both
347 present similar variances, yet s_1 varies proportionally more than s_2 . Additionally,
348 variation in s_2 is constrained by the maximum possible survival, which means that in
349 some time intervals, no individuals died ($survival = 1.0$). A possible solution for such
350 issues is rescaling variance by the maximum possible variance (Morris and Doak 2004,
351 Morris *et al.* 2011). However, there is still no consensus on whether this is the best
352 practice as different rescaling methods provide different results (Bjørkvoll *et al.* 2016,
353 McDonald *et al.* 2017). Nevertheless, this is not a problem for our framework once vital
354 rate variance is weighted by its proportional contribution to λ – the elasticity, a
355 comparable metric between any kinds of demographic processes (Haridas and
356 Tuljapurkar 2005).

357 **Independent and identically distributed (iid) variables:** A common
358 assumption in correlative analyses is the iid, which assumes that all demographic
359 processes are independent from each other (Zar 2010). However, this might often not
360 hold, since many vital rates can be linked by trade-offs (Doak et al. 2005). Thus, the

361 selection pressure on a given demographic process (*e.g.* promoting variation) might
 362 affect other demographic processes in the opposite direction (Doak et al. 2005, Doak
 363 and Morris 2010). Since the data are not iid, the analytical framework must not be
 364 constrained by this assumption. In turn, our framework computes $\Sigma E_{a_{ij}}^{S^\mu}$ and $\Sigma E_{a_{ij}}^{S^\sigma}$,
 365 which inherently capture environmental and trade-off related variance. Additionally, the
 366 second-order derivatives (step 3), may also assess the force and direction of natural
 367 selection in trade-offs which is a potential source of correlation between different
 368 demographic processes (cross-correlative second-order derivative, not described here
 369 but see Caswell 1996, 2001, Shyu and Caswell 2014).

370 **Life histories × demographic processes or patterns × causality:** Correlative
 371 analyses fail to provide a formal link between *processes* (or *causal mechanisms*) and
 372 *patterns* (Shipley 1999), especially because different demographic processes, which are
 373 under different selective pressures, are analyzed as part of the same pattern (Doak *et al.*
 374 2005). For instance, Doak *et al.* (2005) demonstrate that even if high temporal variation
 375 in most of the demographic processes reduces λ , the variation of one or a few vital rates
 376 might have an opposite (and positive) contribution to λ . Mixing demographic processes
 377 under different evolutionary pressures in simple correlative analyses limits our
 378 understanding of the behavior of each demographic process and might lead to finding
 379 no pattern at all. Indeed, this might be a potential explanation of why most of the
 380 coefficients of correlation are close to zero in one of the most comprehensive uses of
 381 correlation analyses assessing DBH and DLH in plants by McDonald *et al.* (2017).

382 **Equal weight:** Correlative analyses (Spearman's correlation) are equally
 383 sensitive to demographic processes with high and low contributions to population
 384 growth rate. However, demographic processes with low contributions to population
 385 growth rate are free to vary under the predictions from the DBH and DLH (Doak *et al.*

2005). In this sense, it is preferable to think the predictions by DBH and DLH as *boundaries*, confining the maximum possible temporal variance of the demographic processes, rather than a trend which they should follow (Fig. 3). By using the step 1 of our framework, demographic processes with low contributions to λ , even if varying freely, should have minor contribution to place populations into the DB-DL continuum (Haridas and Tuljapurkar 2005). This characteristic of $\Sigma E_{a_{ij}}^{S^{\mu}}$ and $\Sigma E_{a_{ij}}^{S^{\sigma}}$ fits conveniently with the predictions posted by the DBH and DLH.

393

Table 1. Performance comparison between the framework proposed here and the largely used approaches to test DBH and DLH (correlative analyses).

	Largely used protocol	New framework proposal	
Limitation \ Approach	correlative analyses	Sum of stochastic elasticity (step 1)	Second-order derivative (steps 2 and 3)
Mean-variance scale	Solved ^{1,2,3,*}	Accounted for	Not relevant
iid	Neglected ⁴	Accounted for	Accounted for
Life history x vital rates	Accounted for but without consensus**	Accounted for, but each step of the present framework has a clear distinction between patterns and processes	
Equal weight	Neglected	Accounted for	Not relevant

*There are multiple ways to solve the scale problem but there is no consensus of which one is the best ([¹]Morris *et al.* 2011, [²]Bjørkvoll *et al.* 2016, [³]McDonald *et al.* 2017)

[⁴] Doak *et al.* 2005.

** Two different approaches exist and are assessed using the same methods *i.e.* multi-species comparative approach and hypothesis testing approach (Box 1).

402

403

404

405 Figure 3. Theoretical relationship between stochastic elasticity and the coefficient of
406 temporal variation under the predictions of DBH and DLH. The predictions from DBH
407 and DLH are depicted in two different ways. Continuous and dashed lines represent a
408 perfect support for the DBH and DLH, respectively, if we assume demographic
409 processes should follow specific trends. Blue and red points represent the positions,
410 where hypothetical vital rates should be placed, considering that natural selection acts
411 by inducing boundaries to temporal variation under DBH and DLH predictions. Areas
412 with co-occurrence of blue and red points together, cannot provide insights about the
413 evolutionary process acting on demographic processes, thus, they represent
414 uninformative areas. Assuming the DBH and DLH as boundaries to temporal variation,
415 the right quadrant is expected to be empty.

416

417 **Demographic buffering in mammals: a case study using the proposed framework**

418 *Study system and predictions*

419 We demonstrate the performance of our framework to assess the DBH vs. DLH
 420 using MPMs from mammal species. Mammals are of special interest here for two
 421 reasons: first, mammalian life histories have been well studied (Gillespie 1977, Stearns
 422 1983, Bielby *et al.* 2007, Jones 2011); and second, some of their populations have
 423 already been assessed in terms of DBH and DLH, particularly for primates (Morris *et*
 424 *al.* 2008, 2011, Reed and Slade 2012, Rotella *et al.* 2012, Campos *et al.* 2017).
 425 Together, the well-studied life histories and previous information about the DBH and
 426 DLH in mammals provide the necessary information to make accurate predictions to
 427 validate the performance of the proposed framework.

428 *First step predictions – demographic responses in mammal life history:* Long-
 429 lived species should be characterized by vital rates that are less dependent on
 430 environmental conditions (Gaillard and Yoccoz 2003, Morris *et al.* 2008, 2011). This
 431 might be particularly evident for primates, which have intense parental care, high
 432 longevities and flexible diets (Jones 2011). These aforementioned traits are expected to
 433 increase species' capacity to buffer the negative effects of the environmental conditions.
 434 In addition, limited litter size imposed by physiological restrictions limits variation in
 435 recruitment even in the bonanza years (Campos *et al.* 2017). Therefore, we predict
 436 minimum variation on demographic processes for primates. The capacity to buffer the
 437 negative effects of the environmental stochasticity and physiological limitations should
 438 vary across the different lineages of mammals. Therefore, at the DL-end, we should
 439 expect short-lived species with a highly variable brood size, as is shown in small
 440 rodents (de Andreazzi *et al.* 2011) (Fig. 4).

441 Ultimately, we tested whether the demographic responses of mammals are
442 related to their longevity and recovery capacities. The relationship between
443 demographic responses has been suggested by Morris *et al.* (2008) but was not
444 supported by McDonald *et al.* (2017). On the other hand, a negative relationship
445 between buffering and recovery rates has been suggested as an ecological reason why
446 demographic buffer should evolve, yet this claim remains untested (Ovaskainen and
447 Meerson 2010, McDonald *et al.* 2017).

448 *Second and third step predictions – patterns of variance and natural selection in*
449 *mammal's life history: **Step 2:*** As we posited in the predictions for step 1, it is unlikely
450 that primates should be placed at the DL-end in the DB-DL continuum. Yet, previous
451 studies have found no support for the idea that the most important vital rates vary less in
452 primates – a pattern expected to support the DBH (Morris *et al.* 2011). Thus, we do not
453 expect clear patterns from the relationship between temporal variation of the
454 demographic processes and their contribution to λ (step 2), particularly for primates
455 (Fig. 5). **Step 3:** This step is more critical in our framework because only humans
456 (Caswell 1996) and a species of perennial herb (Shyu and Caswell 2014) had their
457 demographic processes evaluated in terms of second-order derivatives so far. Yet, as the
458 DBH and DLH predict, we should expect the most important demographic processes to
459 be under stabilizing selection to reduce their temporal variation, supporting the DBH, or
460 to be under disruptive section to increase temporal variation, supporting the DLH (Fig.
461 5).

462

463 *Data and analyses*

464 We used Matrix Population Models from 40 out of 139 studies with mammals
465 available in the COMADRE database v.3.0.0 (Salguero-Gómez *et al.* 2016). These 40

466 populations encompass 34 species from eight taxonomic orders, and have been included
 467 in our analyses because they provide values of demographic processes (a_{ij}) for three or
 468 more different moments, which allowed us to obtain the stochastic elasticity of each a_{ij} .
 469 Although we are aware that not all possible temporal variation in vital rates may have
 470 been expressed within this time period, we assumed this was enough to provide
 471 sufficient variation for population comparison and to test and showcase our framework.
 472 Fortunately, several long-lived species, characterized by low variation in their vital
 473 rates, were studied for a long time (*e.g.* some primates have been studied for more than
 474 20 years – Morris *et al.* 2011). We also removed the populations where either only
 475 survival or only reproduction rates were reported, because we could not calculate the
 476 stochastic growth rate for these populations. A detailed description of the analyzed data
 477 and their original sources is available in supplementary material (Table S1).

478 We included *Homo sapiens* in our analyses because it is the only mammal
 479 species, where second-order derivatives have been applied (Caswell 1996), thus making
 480 them ideal for species comparisons. The data for *Homo sapiens* were pooled from 26
 481 modern populations from different cities to construct a variance. Note that in this case
 482 we are not working with true temporal variance but a spatiotemporal variance instead.

483 A subset of 16 populations, which had their MPMs organized by age (plus *Homo*
 484 *sapiens*), were used to run steps 2 and 3 of our framework. We selected these
 485 populations because the complexity of life histories is summarized only to two
 486 demographic processes: survival (t) and contribution to recruitment of new individuals
 487 (r), which is equivalent to or approximately equal to the mean reproductive output for
 488 each age, depending on the organization of the matrices (Ebert 1999). The advantage of
 489 using such matrices is that there are only two kinds of demographic processes included,
 490 survival and recruitment, instead of multiple transitions from one stage to another. We

491 provide the results for all 40 populations in the supplementary material (Fig. S2). As the
492 non-linear aspect of the contribution of vital rates to individual fitness is often
493 neglected, we decided to provide an example to explore in detail how this nonlinear
494 relationship appears in life histories in the DB-DL context (Fig. S3).

495 To perform the step 1 of our framework, the $\Sigma E_{a_{ij}}^{S^{\sigma}}$ and $\Sigma E_{a_{ij}}^{S^{\mu}}$, we followed
496 Tuljapurkar *et al.* (2003). We checked if the position of species within the DB-DL
497 continuum is correlated to longevity (here represented by generation time) and recovery
498 rate (represented by damping ratio) using simple Spearman's correlations. Generation
499 time and damping ratio were extracted using the *Popbio* package (Stubben 2007). To
500 perform step 2 of our framework, we calculated the coefficient of temporal variation of
501 each demographic process corrected by its maximum variance, as suggested by Morris
502 *et al.* (2011) (Box 2), and plotted the variance against the respective deterministic
503 elasticity, also extracted using the *Popbio* package. All analyses were performed using
504 R version 3.5.1 (R Core team, 2018).

505 Finally, to perform the step 3 of our framework, the second-order derivatives
506 were adapted from *demogR* (Jones 2007) following Caswell (1996) and applied for the
507 mean MPM. Most contributive demographic processes usually have higher absolute
508 values of second-order derivative (Carslake *et al.* 2008) as they are expected to be under
509 stronger pressure of natural selection (Brodie *et al.* 1995, Pfister 1998, Benton and
510 Grant 1999). On another hand, second-order derivative rarely equals zero for the
511 demographic processes, even for those less contributive demographic processes
512 (Carslake *et al.* 2008, McCarthy *et al.* 2008, Shyu and Caswell 2014). However, less
513 contributive demographic processes are either less important or more prone to have
514 neglectable curvature (particularly because they are expected to be under less pressure
515 of the natural selection [Pfister 1998]). As there is no approach to assess whether a

second-order derivative is significantly different from zero or not (see McCarthy *et al.* 2008), we arbitrary rounded the values of second-order derivative for the first decimal place and considered zero as non-informative.

Results

We ranked 40 populations from 34 species according to the cumulative impact of variation in demographic processes on λ_s using the first step of our framework ($\Sigma E_{a_{ij}}^{S^\sigma}$ and $\Sigma E_{a_{ij}}^{S^\mu}$). We show both values in Figure 4, but as the terms $\Sigma E_{a_{ij}}^{S^\sigma}$ and $\Sigma E_{a_{ij}}^{S^\mu}$ are complementary and add up to 1, we only discuss the values from of $\Sigma E_{a_{ij}}^{S^\sigma}$ for simplicity. Additional information is provided in the supplementary material (Table S1). The smallest contribution of variation in vital rates (*i.e.* maximum value of $\Sigma E_{a_{ij}}^{S^\sigma}$, note that $\Sigma E_{a_{ij}}^{S^\sigma}$ ranges from 0 to -1), meaning a less environmentally-dependent life history, was assigned to the Northern muriqui (*Brachyteles hyphoxantus*, Primates) ($\Sigma E_{a_{ij}}^{S^\sigma} = -0.09 \times 10^{-4} \pm 0.12 \times 10^{-4}$) (mean $\pm$ standard deviation) and the most environmentally-dependent population was the stoat (*Mustela erminea*, Carnivora) ($\Sigma E_{a_{ij}}^{S^\sigma} = -0.35 \pm 0.02$).

All 14 primate populations were posited at the DB-end of demographic responses to environmental stochasticity, occupying the upper-left corner of the DB-DL continuum (Fig. 4). Other species in groups such as Carnivora (N = 10) and Artiodactyla (N = 5) are spread across the DB-DL continuum (Fig. 4). Our findings support that life histories with longer generation time are less affected by the environmental stochasticity, $|\Sigma E_{a_{ij}}^{S^\sigma}|$ (Spearman's correlation, $\rho = -0.83$, $P < 0.01$), which means, more buffered. On another hand, life histories more dependent of the environmental stochasticity have also higher recovery capacities, $|\Sigma E_{a_{ij}}^{S^\sigma}|$ (Spearman's

538 correlation, $\rho = 0.45$, $P = 0.01$). These results are in concordance with the predictions
539 from step 1 of our framework.

540 As we predicted for the step 2 (graphical inspection), we could not observe a
541 clear negative correlation between the contribution to λ from separate demographic
542 processes and their temporal variation. Particularly for primates, with the lack or minor
543 temporal variation in demographic processes, an almost flat trend was created for most
544 of the analyzed populations, *e.g.* Northern muriqui, and Mountain gorilla (*Gorilla*
545 *beringei*) (Fig. 5, S2). Yet, these abovementioned populations were all placed into the
546 extreme DB-end using the first step of our framework ($\Sigma E_{a_{ij}}^{S^{\sigma}}$ and $\Sigma E_{a_{ij}}^{S^{\mu}}$). Such result
547 highlights the importance of a clear definition of the expectations and the importance to
548 choose the right method to assess the aspects of the demographic strategy in the wildlife
549 populations. A full discussion is provided below.

550 By using the second-order derivative (step 3), our framework explicitly assessed
551 the evolutionary forces of natural selection acting on each demographic process.
552 However, no clear pattern arose from this step (Fig. 5, S2). Instead, we could identify
553 some evidence of stabilizing or disruptive selection in almost one half of demographic
554 processes (47% and 23 % respectively), mainly mixed within each life history (Fig S4).
555 For instance, evidence of disruptive and stabilizing selection is present in the most
556 important demographic parameters of White face capuchin monkey (*Cebus capucinus*),
557 the rhesus monkey (*Macaca mulata*), and the tamar wallaby (*Macropus eugenii*)
558 populations (Fig. 5, S4). We also use these populations to exemplify how variations in
559 some of the most important demographic processes determine the long-term mean
560 fitness (λ_s) (Fig. S3). Only a few populations, like humans and Columbian ground
561 squirrel (*Urocyon colombianus*), presented negatives values of second-order
562 derivatives for all most important demographic processes – a pattern expected by DBH

563 (Fig. 3, 5). Similarly, only a few populations (*e.g.* killer whale [*Orcinus orca*])
 564 presented all most important demographic processes under disruptive selection –
 565 evidencing DLH (Fig. 5, S4). A general profile on the frequency of what kind of natural
 566 selection the demographic processes are under is provided in the supplementary
 567 material (S4).

568

569

570 Figure 4. Results of the sum of stochastic elasticities with respect to their variance $\Sigma E_{a_{ij}}^{S^{\sigma}}$
571 and mean $\Sigma E_{a_{ij}}^{S^{\mu}}$, as suggested by our framework (step 1), ranking the 40 populations
572 from 34 species of mammals from the COMADRE database onto a DB-DL continuum
573 from more buffered (top left corner) to more labile (bottom right corner). Colors
574 represent different taxonomic orders with Primates occupying the top left corner.
575 Primate populations show the highest capacity to buffer environmental stochasticity, as
576 expected.

577

578

579 Figure 5. Results from steps 2 and 3 of the proposed framework (see Fig. 2B,C). The

580 16 populations presented here are those MPMs built by ages available in the

581 COMADRE database. Different shapes represent different demographic processes

582 (survival and recruitment). As in Figure 2B (step 2), the coefficient of temporal

583 variation of each demographic process is plotted against its deterministic elasticity (see

584 Box 1,2). We complete the graphical information with the value of the second-order

585 derivative (denoted by size) and the direction of natural selection (denoted by color)

586 acting on each demographic process represented by a specific matrix element. Full

587 results are presented in supplementary material (Fig. S2).

588

589 Discussion

590 Our framework allows researchers to detect, quantify, and compare the extent to which
 591 natural populations are demographically buffered or labile in the environment, as well
 592 as the evolutionary processes shaping this capacity to buffer or track the environmental
 593 stochasticity (Fig. 2). In addition, our framework enables the development of an explicit
 594 link between the demographic buffering hypothesis (DBH; Pfister 1998) and the
 595 demographic labile hypothesis (DLH; Koons et al. 2009), and key evolutionary
 596 concepts such as disruptive and stabilizing selection (Fig. 2C). Below, we discuss the
 597 performance and contribution provided by each step of our framework to unveil the
 598 patterns and processes behind the DB-DL perspective.

599

600 *Framework performance*

601 By using the sum of stochastic elasticity of the stochastic population growth rate
 602 with respect of the mean ($\Sigma E_{a_{ij}}^{S^{\mu}}$) and variance ($\Sigma E_{a_{ij}}^{S^{\sigma}}$, step 1), our framework supports
 603 the existing link between species' buffering capacity, their capacity to recover after
 604 disturbances, and their longevity (Boyce *et al.* 2006, Morris *et al.* 2008, McDonald *et*
 605 *al.* 2017). Particularly for the recovery rate, our results represent the first empirical
 606 evidence between species' recovery capacity and the DB-DL perspective. This
 607 particular result signifies an important gain, as both, the DBH and DLH, are mainly
 608 considered in terms of species' capacity to track environmental conditions - particularly
 609 for the DL-end's species (*e.g.* McDonald *et al.* 2017, Hilde *et al.* 2020). In terms of the
 610 relationship between longevity and the DB-DL continuum, our findings support recent
 611 work. Morris *et al.* (2008), also using $\Sigma E_{a_{ij}}^{S^{\sigma}}$ and $\Sigma E_{a_{ij}}^{S^{\mu}}$, found that longevity determines a

species' position along the DB-DL continuum for 36 species of plants, mammals, and other vertebrates. Together, the emerging evidence is starting to indicate that life-history traits should drive the species' position in the DB-DL continuum regardless of the taxonomic group. It is worth pointing out that other attempts, specifically those using correlative analyses (*e.g.* Morris *et al.* 2011, Reed and Slade 2012, McDonald *et al.* 2017), did not reach the same conclusions.

The contrasting results of the correlative analyses versus the $\Sigma E_{a_{ij}}^{S^{\sigma}}$ and $\Sigma E_{a_{ij}}^{S^{\mu}}$, highlight the importance of carefully defining what should be expected for buffered or labile life histories. By clearly stating what we should expect based on the DBH and DLH, our framework using the $\Sigma E_{a_{ij}}^{S^{\sigma}}$ and $\Sigma E_{a_{ij}}^{S^{\mu}}$ (step 1 of our framework; Fig. 2), ranks species on a DB-DL continuum even when all demographic processes present low (or minimum) temporal variance. Temporal variance in vital rates is a necessary component to assess the DBH and DLH predictions and to rank species by using correlative analyses. Yet, several populations – particularly from highly buffered species – should present low (or minimal) temporal variance (*e.g.* Morris *et al.* 2011). A flat trend between temporal variation of vital rates and their contributions to λ might arise if all vital rates present similar and low temporal variation, which cannot be interpreted in terms of DBH and DLH using correlative analyses. Examples of flat or quasi-flat trends appear several times when visually representing the temporal variation of demographic processes and their contributions to λ . Such a pattern is not surprising for primates, where prolonged parental care and limited brood-size keep juvenile survival and adult reproductive rates constant in good or bad years (Morris *et al.* 2011; Campos *et al.* 2017, Salguero-gómez 2021).

Finally, the second-order derivative, step 3 in our framework (Fig. 2), reveals that the role of natural selection shaping temporal variation in vital rates is much more

637 complex than expected by DBH and DLH. Indeed, we found that demographic
638 processes within a population are often under a mix of stabilizing and disruptive
639 selection - a pattern already suggested by Doak *et al.* (2005). Two findings here deserve
640 further attention: firstly, stabilizing selection is not universal but is still dominant in the
641 most important demographic processes. In fact, evidence for demographic processes
642 under the influence of stabilizing selection might reach up to 46%, if we consider only
643 those 25% of most contributing demographic processes in the life-histories. Such a
644 result might help explain why evidence for the DBH has been dominant in the literature
645 (see McDonald *et al.* 2017; Hilde *et al.* 2020). Secondly, we report evidence of
646 beneficial variation - positive values of second-order derivative (U-shaped), even for
647 most important vital rates with low temporal variation. Beneficial temporal variation in
648 most important vital rates was suggested by Koons *et al.* (2009), particularly for short-
649 lived organisms. Here, we show that natural selection might also increase the variance
650 in demographic parameters in long-lived organisms. We found such pattern particularly
651 for primates where most important demographic processes are the survival of oldest
652 individuals (*e.g.* White face capuchin monkey [*C. capucinus*]). This result is probably a
653 consequence of natural selection promoting longer lifespans in some populations, like
654 those of primates, since we found positive second-order derivatives for adult survival of
655 primates (Caswell 1996, Jones 2011, Jones and Tuljapurkar 2015, Colchero *et al.* 2016).
656

657 *General insights: challenges and future directions*

658 Investigating what mechanisms drive species' positioning along the DB-DL
659 continuum is a promising avenue of further investigation. Our results from step 1, $\Sigma E_{a_{ij}}^{S^{\sigma}}$
660 and $\Sigma E_{a_{ij}}^{S^{\mu}}$, show that demographic buffering is a stronger pattern in Primates than
661 Carnivora and Artiodactyla, for example. This pattern in some but not other taxa

662 challenges the view that demographic strategies may not be predicted via phylogenetic
663 distance as suggested by Morris *et al.* (2008). While we did not test this hypothesis
664 explicitly here, however, our trait-based prediction to species' buffering capacity
665 supports the idea that more phylogenetically related species (or species with more
666 similar traits) should present more similar buffering capacities. Indeed, the clustering of
667 Primates but not Carnivora – a widespread taxa in terms of longevity and reproduction
668 rate (van de Kerk *et al.* 2013) – supports the idea that similar species should be placed
669 closer on the DB-DL continuum. We suggest further research should focus on exploring
670 how the DB-DL continuum manifests across the Tree of Life and the role that morpho-
671 physiological and life-history traits play in determining the demographic strategies of
672 these species.

673 The insights provided by the second-order derivatives used in our framework
674 (step 3) represent an important step to integrate ecological and evolutionary
675 implications of selection acting on vital rate temporal variance. The contribution
676 provided by the second-order derivatives was critical to link the evolutionary
677 predictions posited by the DBH and DLH (Pfister 1998, Gaillard and Yoccoz 2003,
678 Hilde *et al.* 2020). Moreover, the second-derivatives provide the necessary information
679 when simple linear relationship fails to predict the effect of temporal variation
680 (perturbation) of a given demographic processes to the mean fitness (Carslake *et al.*
681 2008, Shyu and Caswell 2014). We suggest the second-order derivatives to become
682 more integrated into the ecological and evolutionary aspects of the demographic
683 analyses with the attempt to link trait-based demographic models. For example, Integral
684 Projection Models (IPMs; Easterling *et al.* 2000) usually use continuous traits (*e.g.* size)
685 as a proxy to predict survival and fecundity (Ellner *et al.* 2016). As such, the same

686 approach presented here might be adaptable to assess the evolutionary forces shaping
687 the temporal variation of continuous traits used to build the IPMs.

688 Regardless to the potential of second-order derivatives in stochastic
689 demography, their application is still rather limited (but see Caswell 1996, Carslake *et*
690 *al.* 2008, Shyu and Caswell 2014, 2016), and has for the most part focused on
691 methodological aspects (*e.g.* Caswell 1996, Shyu and Caswell 2014). However, despite
692 the progress in the field since the implementation of the second-order derivatives for
693 structured population models led by Caswell (1996), this method had not yet been
694 applied interspecifically for comparative purposes. Thus, in order to make such
695 comparison, we designed a specific profile of each life history based on the
696 characteristics of the second-order derivative values to make them comparable. Despite
697 the success of our approach to perform descriptive analyses, this approach offer limited
698 statistical inference and remains a challenge for the future.

699

700 **Conclusions**

701 Both, the Demographic Buffering Hypothesis (DBH) and the Demographic Lability
702 Hypothesis (DLH) have become important pieces of an ecological puzzle to predict
703 population responses to environmental stochasticity, climate change, and direct
704 anthropogenic disturbances (Pfister 1998, Boyce *et al.* 2006, McDonald *et al.* 2017,
705 Vázquez *et al.* 2017). Yet, the ecological and evolutionary facets of the DBH and DLH
706 remain tangled in different perspectives that could not have been properly assessed by
707 correlative analyses, as done to date. As a consequence, the literature exploring these
708 two hypotheses is full of contradiction (as reviewed in Hilde *et al.* 2020). Even
709 comparing small groups of closely related species (*e.g.* primates [Morris *et al.* 2011,
710 Campos *et al.* 2017], rodents [Reed and Slade 2012], or herbs [Jäkäläniemi *et al.* 2013])

the results can be contradictory. The framework we propose here disentangles the ecological and evolutionary facets of population responses to stochastic environments, and provides the necessary tools to quantify and link them through two steps (sum of stochastic elasticity of the stochastic population growth rate with respect of the mean ($\Sigma E_{a_{ij}}^{S^\mu}$) and variance ($\Sigma E_{a_{ij}}^{S^\sigma}$) and the second-order derivative), in addition to the usual approach to assess the DBH and DLH (Pfister 1998, Morris and Doak 2004, McDonald et al. 2017).

Applied for 40 populations of different species, our framework helps to solidify classic and more recent avenues of research. Particularly, we highlight the capacity to link the DB-DL perspective with life-history traits (*e.g.* generation time), recovery rates and the possibility to link such results to the recent emphasis in linking functional traits and demographic performance (*e.g.* Adler *et al.* 2014, Salguero-Gómez *et al.* 2018). Thus, future investigations should benefit from this framework to explore, for example, how body mass and behavioral traits correlate with different demographic strategies in environmentally stochastic conditions. Furthermore, the usage of second-order derivatives in the DB-DL perspective represents a promising research avenue to explore the role natural selection to shape the temporal variation of vital rates in different taxa.

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737

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883 **Appendix 1 – Data available in COMADRE Version 2.0.1 and results from step 1.**

884 Table S1. present the metadata used in step 1 of our framework and the respective results presented in the paper. The first four columns represent the information from where Matrix Populations Models (MPMs) were
885 extract exactly as presented in COMADRE 2.0.1. Column titles differ from the database as “SpeciesAuthorComadre” is equivalent to “SpeciesAuthor” and “SpeciesName” is equivalent to “SpeciesAccepted” in
886 COMADRE 2.0.1. The remaining columns present the results of step 1, where we present the raw values of $\Sigma E_{a_{ij}}^{S^{\mu}}$ and $\Sigma E_{a_{ij}}^{S^{\sigma}}$, their respective standard deviation, population growth rate λ , number of available matrices
887 (# matrices), generation time and damping ratio for each population. For ByAge, assign “TRUE” for MPMs built by age or “FALSE” if otherwise.

SpeciesAuthorComadre	SpeciesName	CommonName	Order	$\Sigma E_{a_{ij}}^{S^{\mu}}$	$\Sigma E_{a_{ij}}^{S^{\mu}}$ (sd)	$\Sigma E_{a_{ij}}^{S^{\sigma}}$	$\Sigma E_{a_{ij}}^{S^{\sigma}}$ (sd)	# matrices	λ	Generation time	Damping ratio	ByAge
Homo_sapiens_subsp._sapiens	<i>Homo sapiens sapiens</i>	Human	Primates	1.003	0.003	1.003	0.003	13.000	1.064	5.499	NA	TRUE
Alces_alces	<i>Alces alces</i>	Moose	Artiodactyla	1.001	0.001	1.001	0.001	13.000	1.205	10.628	2.168	TRUE
Antechinus_agilis	<i>Antechinus agilis</i>	Agile antechinus	Dasyuromorphia	1.111	0.111	1.111	0.044	2.000	0.931	2.153	NA	FALSE
Brachyteles_hypoxanthus	<i>Brachyteles hypoxanthus</i>	Northern muriqui	Primates	1.000	0.000	1.000	0.000	12.000	1.051	37.205	1.244	TRUE
Callospermophilus_lateralis	<i>Callospermophilus lateralis</i>	Golden-mantled ground squirrel	Rodentia	1.054	0.054	1.054	0.040	9.000	2.052	NA	3.955	TRUE
Cebus_capucinus	<i>Cebus capucinus</i>	White faced capuchin monkey	Primates	1.000	0.000	1.000	0.000	11.000	1.021	29.363	1.391	TRUE
Cercopithecus_mitis	<i>Cercopithecus mitis</i>	Blue monkey	Primates	1.000	0.000	1.000	0.000	14.000	1.036	21.452	1.240	TRUE
Eumetopias_jubatus	<i>Eumetopias jubatus</i>	Northern sea lion; Steller sea lion	Carnivora	1.005	0.005	1.005	0.005	2.000	0.904	9.645	NA	FALSE
Felis_catus	<i>Felis catus</i>	Feral cat	Carnivora	1.136	0.136	1.136	0.044	1.000	1.948	5.476	5.135	FALSE
Gorilla_beringei	<i>Gorilla beringei</i>	Mountain gorilla	Primates	1.000	0.000	1.000	0.000	21.000	1.027	38.817	1.239	TRUE
Hippocamelus_bisulcus	<i>Hippocamelus bisulcus</i>	Huemul deer	Artiodactyla	1.002	0.002	1.002	0.002	1.000	0.996	10.452	2.928	FALSE
Lepus_americanus	<i>Lepus americanus</i>	Snowshoe hare	Lagomorpha	1.294	0.294	1.294	0.160	2.000	0.812	2.290	NA	FALSE
Lycaon_pictus	<i>Lycaon pictus</i>	African wild dog	Carnivora	1.100	0.100	1.100	0.060	1.000	1.500	4.149	2.163	FALSE
Macaca_mulatta_3	<i>Macaca mulatta</i>	Rhesus macaque	Primates	1.000	0.000	1.000	0.000	12.000	1.127	14.749	1.616	TRUE
Macropus_eugenii	<i>Macropus eugenii</i>	Tammar wallaby	Diprotodontia	1.013	0.013	1.013	0.013	7.000	0.981	4.872	10.930	TRUE
Marmota_flaviventris_2	<i>Marmota flaviventris</i>	Yellow-bellied marmot	Rodentia	1.007	0.007	1.007	0.007	4.000	0.890	4.210	1.489	FALSE
Marmota_flaviventris_3	<i>Marmota flaviventris</i>	Yellow-bellied marmot	Rodentia	1.008	0.008	1.008	0.008	4.000	0.921	5.017	3.575	FALSE
Microtus_oeconomus	<i>Microtus oeconomus</i>	Root vole	Rodentia	1.000	0.000	1.000	0.000	14.000	1.028	30.588	4.489	TRUE
Mustela_erminea	<i>Mustela erminea</i>	Stoat	Carnivora	1.334	0.334	1.334	0.114	2.000	1.258	5.803	11.201	FALSE
Orcinus_orca_2	<i>Orcinus orca</i>	Killer whale	Cetacea	1.001	0.001	1.001	0.001	24.000	0.999	28.745	NA	TRUE
Ovis_aries_2	<i>Ovis aries</i>	Soay sheep	Artiodactyla	1.033	0.033	1.033	0.020	3.000	1.099	8.036	NA	TRUE
Pan_troglodytes_subsp._schweinfurthii	<i>Pan troglodytes</i>	Eastern chimpanzee	Primates	1.000	0.000	1.000	0.001	22.000	0.982	37.652	1.132	TRUE
Papio_cynocephalus	<i>Papio cynocephalus</i>	Olive baboon	Primates	1.000	0.000	1.000	0.000	19.000	1.054	21.860	1.289	TRUE
Peromyscus_maniculatus_2	<i>Peromyscus maniculatus</i>	Deer mouse	Rodentia	1.010	0.010	1.010	0.005	2.000	1.107	5.596	1.780	FALSE
Phocarcos_hookeri	<i>Phocarcos hookeri</i>	New Zealand sea lion	Carnivora	1.005	0.005	1.005	0.003	8.000	1.023	9.681	1.256	FALSE
Propithecus_verreauxi	<i>Propithecus verreauxi</i>	Verreaux's sifaka	Primates	1.000	0.000	1.000	0.000	12.000	0.986	21.963	1.376	TRUE
Puma_concolor_8	<i>Puma concolor</i>	Cougar	Carnivora	NA	NA	NA	NA	10.000	1.115	4.806	NA	FALSE
Rattus_fuscipes	<i>Rattus fuscipes</i>	Bush rat	Rodentia	1.246	0.246	1.246	0.029	2.000	1.305	2.023	NA	FALSE
Spermophilus_armatus	<i>Urocitellus armatus</i>	Uinta ground squirrel	Rodentia	1.016	0.016	1.016	0.011	4.000	1.125	3.755	8.020	FALSE
Spermophilus_armatus_2	<i>Urocitellus armatus</i>	Uinta ground squirrel	Rodentia	1.017	0.017	1.017	0.010	3.000	1.095	4.838	2.767	FALSE
Spermophilus_columbianus	<i>Urocitellus columbianus</i>	Columbian ground squirrel	Rodentia	1.036	0.036	1.036	0.025	3.000	1.009	4.508	2.510	FALSE
Spermophilus_columbianus_3	<i>Urocitellus columbianus</i>	Columbian ground squirrel	Rodentia	1.003	0.003	1.003	0.006	3.000	1.200	4.524	NA	TRUE
Ursus_americanus_subsp._floridanus	<i>Ursus americanus</i>	Florida black bear	Carnivora	1.003	0.003	1.003	0.003	2.000	1.020	9.591	1.890	FALSE

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Ursus_arctos_subsp._horribilis_5	<i>Ursus arctos</i>	Grizzly bear	Carnivora	1.001	0.001	1.001	0.001	4.000	1.026	11.558	1.158	FALSE
Ursus_maritimus_2	<i>Ursus maritimus</i>	Polar bear	Carnivora	1.019	0.019	1.019	0.001	2.000	0.941	18.491	1.552	TRUE
Brachyteles_hypoxanthus_2	<i>Brachyteles hypoxanthus</i>	Northern muriqui	Primates	1.000	0.000	1.000	0.001	12.000	1.111	21.278	3.443	TRUE
Cebus_capucinus_2	<i>Cebus capucinus</i>	WhiteNAfaced capuchin monkey	Primates	1.000	0.000	1.000	0.001	11.000	1.059	18.977	3.636	TRUE
Chlorocebus_aethiops_2	<i>Chlorocebus aethiops</i>	Vervet	Primates	1.075	0.075	1.075	0.001	5.000	1.187	5.694	3.508	FALSE
Erythrocebus_patas	<i>Erythrocebus patas</i>	Patas monkey	Primates	1.051	0.051	1.051	0.001	5.000	1.128	3.499	2.291	FALSE
Gorilla_beringei_subsp._beringei	<i>Gorilla beringei</i>	Mountain gorilla	Primates	1.000	0.000	1.000	0.001	21.000	1.053	24.536	4.161	TRUE

894 Figure S2. Results from steps 2 and 3 for all populations analyzed (see fig. 2B,C) in this study. Differently to figure 5, which only uses
895 MPMs built by age with two kinds of transitions a_{ij} – survival and recruitment, figure S2 presents MPMs built with all sorts of categories
896 if they matched the criteria informed in *data and analyses* section. Therefore, instead of simple survival rates, we might disentangle it in
897 other demographic processes as self-loops (retain in same stage) and jump for next stage (growth) are depicted in “stage transition”. Here
898 we opted to simply inform what is a transition from a stage to another and what is contribution to recruitment. Moreover, differently to
899 figure 5, common species names are paired with their respective identification in the “SpeciesAuthor” column in COMADRE database.
900 Please note that the important results present in this figure have been covered by the discussion of results for figure 5.

903 **Appendix 3**

904 Figure S3. Example of nonlinear contribution to long-term mean fitness (λ) by two demographic processes in three populations analyzed in
905 figure 5. The x-axis shows multiple simulated values of recruitment and survival with their respective contribution to long-term mean
906 fitness (λ) on the y-axis. Vertical dashed lines show the recruitment and survival values from the mean MPM, as well as the corresponding
907 value of λ (horizontal dashed line).

910 Figure S4. Most of life histories present mix of stabilizing and disruptive selection in their most important demographic processes and its
911 proportion are presented for all life histories analyzed. From right to left, we present the proportion of disruptive and stabilizing selection
912 acting on all demographic processes in a life-history (all non-zero entries in the MPM), followed by the proportion of each kind of natural
913 selection for those 50% and 25% of most contributive demographic processes. At the end of each column the overall result including all
914 life-histories is presented. Each life-history analyzed is informed at the left by species common name followed by its respective
915 identification in the “SpeciesAuthor” column in COMADRE database.