

1      **Population responses to environmental stochasticity are primarily driven by**  
2      **survival-reproduction trade-offs and mediated by aridity**

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20     Figures: 4

21    **Summary**

22    Forecasting responses of natural populations to increasingly stochastic environments is a major  
23    challenge in Ecology and Conservation Biology. We now know that populations can modulate  
24    how their vital rates (*e.g.*, survival, reproduction) change through time to minimise the negative  
25    impacts of environmental stochasticity. However, despite the important analytical and theoretical  
26    advances that have led to this knowledge, we still do not know (1) how much this ability of natural  
27    populations to buffer against environmental stochasticity can vary in nature, nor (2) the drivers of  
28    these strategies, with likely candidates including the environmental regimes themselves, as well as  
29    the life history traits and phylogenetic ancestry of the species of interest. To address these  
30    questions, we parameterised a Bayesian generalised linear mixed model with high-resolution vital  
31    rate data from 134 natural populations across 89 species of plants and animals. We show that  
32    population responses to environmental stochasticity vary three orders of magnitude along a  
33    ‘demographic buffering continuum’. Furthermore, the position of a given population along said  
34    continuum is predicted by a survival-reproduction trade-off and by the degree of aridity the  
35    population experiences. Our findings open a promising avenue of research to improve ecological  
36    forecasts and management of natural populations in the Anthropocene.

37

38    **Keywords:** Climatic change, Demographic buffering, Environmental canalisation, Fast-slow  
39    continuum, Life history, Reaction norm.

40 **1. Introduction**

41 The long-term viability of natural populations is largely determined by environmental  
42 stochasticity<sup>1,2</sup>. Climate change projections anticipate a global increase in not only the mean of  
43 key abiotic drivers (e.g., temperature, precipitation), but also their temporal variance<sup>3</sup>. Crucially,  
44 increased environmental stochasticity has already brought about important eco-evolutionary  
45 challenges for the performance and viability of natural populations<sup>2,4</sup>, and has been identified as a  
46 major driver of biodiversity loss worldwide<sup>5</sup>. As such, understanding whether and how populations  
47 minimise the expected negative effects of environmental stochasticity has become a primary  
48 mission of Ecology, Evolution, and Conservation Biology<sup>6</sup>.

49 Half a century of research examining how species' life history strategies are shaped by  
50 natural selection to cope with environmental stochasticity have led to the establishment of two  
51 major axes of life history variation: the fast-slow continuum<sup>7,8</sup> and the reproductive strategies  
52 continuum<sup>9–11</sup>. The fast-slow continuum ranks organisms according to a development-survival  
53 trade-off from fast growing, short-lived organisms to slow growing, long-lived ones<sup>7</sup>. In contrast,  
54 the reproductive strategy continuum, which is orthogonal to the fast-slow continuum<sup>12–14</sup>,  
55 categorises organisms based on the length of their reproductive window, from single (*i.e.*,  
56 semelparous) to multiple reproductive bouts (*i.e.*, iteroparous)<sup>9,15</sup>. Recent advances in  
57 biodemography have linked species at the slow-end of the fast-slow continuum to a greater  
58 capacity to buffer the negative impacts of environmental variation mediated by natural selection<sup>16–</sup>  
59 <sup>18</sup>. This so-called demographic buffering<sup>17,19</sup> is accomplished by reducing the temporal variance  
60 of those vital rates (e.g., survival, growth, reproduction) that contribute most to stochastic  
61 population growth rate ( $\lambda_s$ ). However, the demographic buffering hypothesis<sup>17,19</sup> does not account  
62 for the various shapes of environment-vital rate reaction norms<sup>20–22</sup>. For instance, following

63 Jensen's inequality<sup>23</sup>, convex (U-shaped) environment-vital rate reaction norms can result in a  
64 positive effect of vital rate variance on  $\lambda_s$ , whereas linear or concave ( $\cap$ -shaped) reaction norms  
65 lead to a negative effect<sup>21,24</sup>. Importantly, there are limits to the amount of variance that a vital rate  
66 can exhibit without driving a population to local extinction<sup>25</sup>. Altogether, these complementary  
67 parts to the demographic buffering hypothesis remain a major challenge to link life history  
68 continua to populations response to environmental stochasticity in the context of climatic change.

69 Here, we focus on a continuum of vital rate temporal variance to examine how  
70 environmental regimes, key life history traits, and evolutionary history predict the extent to which  
71 natural populations of multicellular organisms can buffer against environmental stochasticity<sup>26</sup>.  
72 Specifically, we parameterise a phylogenetically-corrected Bayesian Generalised Linear Mixed  
73 Model (GLMM) with high-resolution vital rate data from 134 natural populations across 11 animal  
74 and 78 plant species to test the following hypothesis: ( $H_{1a}$ ) Plant and animal populations' responses  
75 to stochastic environments regarding vital rate variance vary widely, but largely overlap along a  
76 continuum of demographic buffering where, on one extreme, temporal variance of governing vital  
77 rates is constrained (*i.e.* more buffered, Fig. 1), while on the other extreme, not at all (less  
78 buffered). Additionally, ( $H_{1b}$ ) the position of species' populations along the demographic buffering  
79 continuum is not predicted by the fast-slow and reproductive strategies continua. Although a study  
80 using 36 populations of different species found that longevity (a life history trait aligned with the  
81 fast-slow continuum<sup>10–12,14</sup>) is a good proxy of demographic buffering<sup>18</sup>, another study with a  
82 greater number of populations and that explicitly accounted for their evolutionary history provided  
83 opposing evidence<sup>27</sup>. However, none of these studies included environmental metrics to explicitly  
84 account for the actual environmental stochasticity faced by the studied population. This key  
85 omission overlooks the potential roles of reproductive strategies, phylogenetic relationships, and

86 environmental regimes on population responses to environmental stochasticity; ( $H_2$ ) phylogenetic  
87 ancestry will play a stronger role in determining demographic buffering capacities in animals than  
88 in plants because morphology and behaviour, strong predictors of a species' demography<sup>28,29</sup>, are  
89 much more conserved across animals than in plants<sup>30,31</sup>; and ( $H_3$ ) the extent to which a natural  
90 population displays demographic buffering will depend on the environmental regime that it has  
91 been exposed to, with higher stochasticity in precipitation and temperature contributing to greater  
92 variances in vital rates, which will place populations toward a less buffered end of said continuum.

93 To test our hypotheses, we first established the existence of a continuum of vital rate variance  
94 from high to low demographic buffering. This continuum emerges when examining how the  
95 observed temporal variance of vital rates has shaped the long-term population performance of each  
96 natural population. To do so, we use the sum of stochastic elasticity of the stochastic population  
97 growth rate  $\lambda_s$  with respect to vital rate temporal variance,  $\sum E_v^\sigma$ . This variable was calculated from  
98 a subset of matrix population models from COMPADRE<sup>32</sup> and COMADRE<sup>33</sup> databases that depict  
99 the demography of populations under natural environmental conditions (see Materials and  
100 Methods for further details on the data selection criteria). Absolute values of  $|\sum E_v^\sigma|$  close to 0  
101 correspond with small effects of the temporal variation of vital rates on population growth rate  $\lambda_s$   
102 (*i.e.*, high demographic buffering), while  $\sum E_v^\sigma$  away from 0 represents a more tangible effect on  
103  $\lambda_s$  (low demographic buffering). Next, we also quantified the responses of our 134 natural  
104 populations to environmental stochasticity in the context of their positions along multiple axes of  
105 variation: the fast-slow and reproductive continua, and environmental stochasticity, using  
106 Principal Component Analyses (PCAs).

107

108 **2. Results**

109 Our 134 examined plant and animal populations unveil a continuum of variance in vital rates that  
110 is highly overlapping between the Kingdoms, as quantified by  $|\sum E_v^\sigma|$ . In fact, we find no evident  
111 distinction in the range of demographic buffering responses to environmental stochasticity  
112 between plants and animals ( $t$ -test = 0.701,  $p$  = 0.495; Figure 1). These findings provide support  
113 for our hypothesis  $H_{Ia}$ , that the responses of natural populations to environmental stochasticity  
114 might be described along a continuum from strongly buffering to not at all, independent of  
115 kingdom. For animals, the variation in demographic buffering ranges from rather low values, such  
116 as  $|\sum E_v^\sigma| = 0.000 \pm 0.045$  (SD) in the Red gorgonian (*Paramuricea clavata*) to  $|\sum E_v^\sigma| = 1.016 \pm$   
117 2.543 in the Woolly sculpin (*Clinocottus analis*). For plants, the demographic buffering ranges  
118 again from low values, like  $|\sum E_v^\sigma| = 0.000 \pm 0.005$  for the Pyrenean violet (*Ramonda myconi*) to  
119 an even higher maximum value than for animals:  $|\sum E_v^\sigma| = 2.014 \pm 3.420$  in the Mexican hat  
120 (*Ratibida columnifera*). For both kingdoms, the position of populations along the demographic  
121 buffering continuum is mainly determined by the temporal variance of survival ( $E_{Survival}^\sigma = 52.0$   
122  $\pm 27.7\%$ ; Figure 2), followed by individual-level growth ( $E_{Growth}^\sigma = 19.6 \pm 20.0\%$ ) and  
123 reproduction ( $E_{Reproduction}^\sigma = 18.5 \pm 26.9\%$ ), with minor contributions from individual-level  
124 shrinkage ( $E_{Shrinkage}^\sigma = 5.54 \pm 10.5\%$ ) and clonality ( $E_{Clonality}^\sigma = 4.33 \pm 17.7\%$ ; Figure 2 and  
125 Table S1).

126 Our analyses provide support for  $H_{Ib}$  in plants, but not in animals. Indeed, the position of  
127 plant populations along the demographic buffering continuum, as quantified by  $|\sum E_v^\sigma|$ , is predicted  
128 by the fast-slow and reproductive strategies continua (Figure 3). However, in plants, the  
129 reproductive strategies continuum is only informative when phylogenetic ancestry is not  
130 considered (Figure 4). Because of the lack of support for  $H_{Ib}$  in animals, we focus our results for

131 plants populations hereafter, but both results are presented (see Fig. 3 and 4). Thus, considering  
132 plants populations, our model without phylogenetic corrections, the interaction between the fast-  
133 slow and reproductive strategy continua (the first two principal component axes of life histories,  
134  $PC_{1LH} : PC_{2LH}$ , respectively; Fig. S1) determines the position of populations along the  
135 demographic buffering continuum (non-phylogenetic corrected MCMCglmm  $|\sum E_v^\sigma|$ ,  
136  $\beta_{PC_{1LH}:PC_{2LH}} = 0.022 [0.001 - 0.042]$ ; posterior mean and 95% credible interval). However, neither  
137 main effects of  $PC_{1LH}$  (fast-slow continuum) nor  $PC_{2LH}$  (reproductive continuum) are significant  
138 ( $\beta_{PC_{1LH}} = -0.017 [-0.039 - 0.005]$ ;  $\beta_{PC_{2LH}} = -0.026 [-0.066 - 0.014]$ ). More importantly, after  
139 controlling for phylogenetic relationships in our data, only the fast-slow continuum remains an  
140 important predictor of  $|\sum E_v^\sigma|$  in plants (phylogenetically corrected MCMCglmm  $|\sum E_v^\sigma|$ ,  
141  $\beta_{\lambda_{PC_{1LH}}} = -0.011 [-0.021 - 0.000]$ ; Figure 3), with no significance for animals. Thus, in agreement  
142 with our hypothesis  $H_{Ib}$ , there is no link between the reproductive strategy continuum and the  
143 contributions of reproduction to the demographic buffering capacity ( $E_{Reproduction}^\sigma$ ), independent  
144 of phylogenetic corrections ( $E_{Reproduction}^\sigma$ ,  $\beta_{\lambda_{PC_{2LH}}} = 0.003 [-0.009 - 0.016]$ ) or not  
145 ( $E_{Reproduction}^\sigma$ ,  $\beta_{PC_{2LH}} = 0.012 [-0.011 - 0.033]$ ; Figure 4). The lack of relationship between the  
146 reproductive strategy continuum and demographic buffering continuum may reflect: (i) the  
147 reduced impact temporal variation in reproduction has on  $\lambda_s$  ( $E_{Reproduction}^\sigma = 18.5 \pm 26.9\%$ ;  
148 Figure 2 and Table S1), and/or (ii) the strong phylogenetic signal in the contribution of  
149 reproduction to  $|\sum E_v^\sigma|$ , at least for plants (Pagel's  $\lambda_{Reproduction} = 0.971 \pm 0.011$ ; Figure 4). This  
150 result suggests that the contribution of reproduction to the populations' responses to environmental  
151 stochasticity is better predicted by phylogenetic ancestry than by life history traits or  
152 environmental conditions.

153        The aforementioned discrepancies between phylogenetically and non-phylogenetically  
154    corrected models support the idea that evolutionary history plays an important role in the  
155    placement of populations along the demographic buffering continuum. However, our results do  
156    not support  $H_2$ , that phylogenetic ancestry would play a stronger role in animals than in plants.  
157    Instead, the values of  $\sum E_v^\sigma$  along the demographic buffering continuum for plants raise a very  
158    strong phylogenetic signal (Pagel's  $\lambda = 0.967 \pm 0.138$ ), while animals have a relatively weak one  
159    (Pagel's  $\lambda = 0.345 \pm 0.230$ ). However, the phylogenetic signal of the contributions of the  
160    underlying vital rates to  $\sum E_v^\sigma$  is variable. For instance, survival has a rather weak phylogenetic  
161    signal for both plants (Pagel's  $\lambda_{survival} = 0.259 \pm 0.106$ ; mean  $\pm$  SD) and animals (Pagel's  
162     $\lambda_{survival} = 0.399 \pm 0.229$ ; Figure 4). A potential reason to explain why the plant demographic  
163    buffering continuum has a higher phylogenetic signal than animals, even if it does not hold for  
164    survival, may be the greater sampled size in plants, which includes some species represented by  
165    multiple populations in our study (Table S2). Consequently, more conservative values of  $\sum E_v^\sigma$   
166    between populations of the same species compared to other species might be promoting a higher  
167    phylogenetic signal in plants. The same relationship might in reality apply to natural populations  
168    of animals, an aspect that we might be able to unveil as the discipline continues to accrue longer,  
169    high-quality vital rate data<sup>35</sup>.

170        Our phylogenetically and non-phylogenetically corrected models both support  $H_3$ , that  
171    populations located in more stochastic environments are positioned towards the low-buffering end  
172    ( $|\sum E_v^\sigma| \gg 0$ ) of the demographic buffering continuum (Fig. 1). In our 134 natural populations,  
173    temporal variation in aridity ( $\beta\lambda_{PC2Env} = 0.033 [0.004 - 0.061]$ ), more so than in temperature  
174    ( $\beta\lambda_{PC1Env} = 0.020 [-0.015 - 0.053]$ ; Figure 3), act as the main determinant of the placement of  
175    populations along the demographic buffering continuum. Moreover, the temporal variation in

176 aridity ( $\beta\lambda_{PC2_{Env}}$ ) outweighs over three-fold the predictive power of the fast-slow continuum  
177 ( $\beta\lambda_{PC1_{LH}}$ ) (posteriors  $|\beta\lambda_{PC2_{Env}} / \beta\lambda_{PC1_{LH}}| = 0.033/-0.011$ ). However, the influence of  
178 environmental stochasticity on population responses depends on the vital rate under consideration.  
179 For example, aridity is the main determinant of the contribution of individual growth to population  
180 responses to environmental stochasticity ( $E_{growth}^\sigma$ ), with more stochasticity in aridity being  
181 associated with lower demographic buffering, at least for plants ( $E_{growth}^\sigma, \beta\lambda_{PC2_{Env}} = -0.006 [-$   
182  $0.012 - -0.001]$ ; Figure 4). In contrast, temperature and aridity act together to determine the  
183 importance of survival ( $E_{survival}^\sigma$ ) on  $\sum E_v^\sigma$  values of plants ( $E_{survival}^\sigma, \beta\lambda_{PC1_{Env}:PC2_{Env}} = -0.028 [-$   
184  $0.045 - -0.010]$ ; Figure 4). These findings likely reflect the greater dependence of plants, as sessile  
185 organisms, on the capacity to survive and grow under heatwave-induced drought events<sup>36</sup>  
186 compared to the – mostly mobile – animal species examined here.

187

### 188 **3. Discussion**

189 The fast-slow and reproductive strategies continua of life history traits have long dominated  
190 predictions of species adaptation to environmental conditions<sup>37,38</sup>. However, these axes have  
191 proven limited in predicting population responses to environmental stochasticity<sup>39–41</sup>. Over the past  
192 two decades, a novel framework to examine population responses to environmental stochasticity  
193 has emerged based on the idea that natural selection must canalise the temporal variation in vital  
194 rates to buffer against the expected negative impacts of environmental stochasticity<sup>19,42</sup>, a  
195 prediction referred to as the ‘demographic buffering hypothesis’<sup>19,42</sup>. Despite significant progress  
196 in the pertinent theory<sup>17</sup> and praxis<sup>43</sup>, we still lack a solid understanding of the drivers of population  
197 responses to environmental stochasticity, their relationship to the well-known fast-slow and

198 reproductive strategies continua, and the role of evolutionary history and environmental  
199 regimes<sup>17,27</sup>. Here, we provide a critical assessment of this gap in knowledge and report several  
200 key findings: (i) Plant and animal populations fall along a single axis, with significant overlap, that  
201 quantifies their responses to environmental stochasticity, from more to less demographically  
202 buffered; (ii) This response can be defined by species' life history (*i.e.*, fast-slow and reproductive  
203 strategies), phylogenetic relationships, and environmental conditions; however, these relationships  
204 are complex; (iii) When phylogenetic relationships are taken into account, the fast-slow continuum  
205 – but not the reproductive strategies continuum – remains as an important predictor of species  
206 response to environmental stochasticity; (iv) Yet, the predictive power of the fast-slow continuum  
207 on the ability of a population to buffer against the environment is outweighed by a key aspect of  
208 environmental stochasticity: variation in aridity. Finally, (v) species' responses to environmental  
209 stochasticity are strongly cemented on evolutionary history, but, contrary predictions<sup>31</sup>, the  
210 phylogenetic signal is stronger in plants than in animals.

211 In our study, environmental stochasticity outweighs the role of life history traits in  
212 predicting the buffering capacities of natural populations. This effect is explained by the larger  
213 influence of survival on species' buffering capacity, which we also characterise as the vital rate  
214 with lowest phylogenetic conservatism in our study, well above growth, shrinkage, and  
215 reproduction. As consequence, the position of a given population along the demographic buffering  
216 continuum reflects its capacity to buffer variation in survival, a result that supports the well-known  
217 challenge of predicting survival of animals and plants in a stochastic environment<sup>36,41</sup>. Here, we  
218 highlight three major challenges to use evolutionary history and life history traits to predict plant  
219 and animal survival in a stochastic environment. First, organisms may possess life history traits  
220 that were once advantageous in the ancestral environments but that, given the fast changing

221 climate<sup>3</sup>, are no longer beneficial. For instance, some species have evolved specific windows for  
222 recruitment or migration that were adaptive in environments with predictable fluctuations, but are  
223 maladaptive in current/future unpredictable environments<sup>44</sup>. Second, individual responses to  
224 environmental stochasticity are highly heterogeneous and tend to be determined by their capacities  
225 to obtain and conserve energy rather than their evolutionary life history<sup>41</sup>. Third, covariation  
226 between physiological and morphological traits can amplify or dampen the impact of  
227 environmental stochasticity on individual performance<sup>36,45,46</sup>. Consequently, environmental  
228 stochasticity may result in nonlinear responses that pose important challenges for ecological  
229 forecast<sup>21,47</sup>. Together, these challenges likely weaken the predictive power of the fast-slow and  
230 reproductive strategies axes, which do not explicitly consider demographic variation. As such, we  
231 argue that these life history axes reflect how species have evolved to cope with past environmental  
232 stochasticity rather than current or future pressures populations – are likely to – face. On the other  
233 hand, these complex responses exemplify the numerous evolutionary processes that can influence  
234 temporal variation in vital rates, upon which the demographic buffering hypothesis was  
235 developed<sup>22,48</sup>. The existence of a demographic buffering continuum that quantifies the temporal  
236 variance in vital rates, as we report here, is a promising tool to generate new insights regarding  
237 which and how populations respond to environmental stochasticity. It is worth noting that, for  
238 plants and animals, populations with higher long-term performance ( $\lambda_s$ ) are located at intermediary  
239 levels of temporal variance in their vital rates, suggesting that some variance is potentially  
240 beneficial, but too much may not be.

241 Despite being subject to stronger phylogenetic conservatism, the contribution of  
242 reproduction to population response to environmental stochasticity is relatively low compared to  
243 other vital rates. This finding contrasts with the high influence but low phylogenetic conservatism

244 of survival. Together, these findings call for more research exploring how survival-reproduction  
245 trade-offs will shape population performance in the Anthropocene. For instance, recent studies  
246 have shown how reductions in survival might be compensated by increases in reproduction, a  
247 phenomenon known as demographic compensation<sup>49,50</sup>. Although a growing body of literature has  
248 supported the widespread existence of demographic compensation among natural populations<sup>50,51</sup>,  
249 their capacity to compensate against the negative impact of environmental stochasticity remains  
250 poorly understood<sup>49</sup>. Given our finding of low contribution but high predictable influence of  
251 reproduction on population responses to environmental stochasticity, one could expect limited  
252 contributions of reproduction in this compensation process as well as great predictability of their  
253 compensation capacity. Investigating such a questions is particularly key to predict population  
254 responses to climate change<sup>52</sup>, particularly under uncertain increasing in environmental  
255 stochasticity<sup>3</sup>. Additionally, we suggest that, because the effects of reproduction on population  
256 responses to environmental stochasticity are highly predictable by evolutionary history, there is an  
257 opportunity to improve the parameterisation and accuracy of demographic models in population  
258 viability analyses<sup>53</sup>. This opportunity includes models examining early impacts of exploitation,  
259 such seed harvesting<sup>54</sup>. When survival (most important and less predictable vital rate) cannot be  
260 fitted in the model parameterization, reducing uncertainty in other vital rates such reproduction is  
261 imperative<sup>53</sup>. Our findings show promising avenue of research in this direction.

262 It is critical to recognise that our framework, using the sum of stochastic elasticities of the  
263 stochastic population growth rate  $\lambda_s$  with respect to vital rate temporal variance,  $\sum E_v^\sigma$ , has two  
264 areas for improvement. First, the theoretical aspect related to the buffering hypothesis and its  
265 alternative hypothesis – the demographic lability hypothesis<sup>19,21,48</sup> – remains poorly understood.  
266 This gap of knowledge hampers a direct link between to the demographic buffering continuum of

267 variance explored in this study. The demographic buffering and lability hypotheses have been  
268 understood in terms of underlying evolutionary mechanisms such as canalising by stabilising  
269 selection resulting in buffering, or boosting the temporal variance by disruptive selection in  
270 lability<sup>19,21,48</sup>. Ultimately, these evolutionary processes might result in the observed patterns of  
271 vital rate variance, from constraints (if buffered) to boosting (if labile), which have been the  
272 analytical focus of the attempts to test these hypotheses in recent years<sup>19,27,43</sup>. However, such  
273 underlying evolutionary mechanisms of buffering and lability have only been inferred, instead of  
274 being directly assessed<sup>48</sup>. So far, the only two attempts to explicitly identify and quantify the  
275 underlying evolutionary mechanisms behind demographic buffering and lability (nonlinear  
276 indexes<sup>22</sup> and second-order derivatives<sup>48</sup>) have not considered a critical component: the observed  
277 temporal variation and its impact on population growth rate. Our approach captures only the  
278 temporal variation and its impact on population performance, which represents their overall  
279 demographic buffering capacity, but not the underlying evolutionary mechanisms (*i.e.*, stabilizing  
280 vs. disruptive selection) driving this temporal variation<sup>48</sup>. Thus, while our framework is not the  
281 final stop of this important line of enquiry, our framework provides a unique set of opportunities  
282 to complement recent evolutionary metrics such as nonlinearity indexes<sup>22</sup> and second-order  
283 derivatives<sup>48</sup>. Further studies may integrate such metrics into the present framework to link the  
284 forces of natural selection and their effects on the current and future performance of natural  
285 populations.

286 A second area for improvement is the suboptimal representation of long-term demographic  
287 studies across taxonomies and geographies required for comparative demographic studies. The  
288 existing databases we use here, though state-of-the-art in regards to number of demographic  
289 studies, still remains biased toward perennial species in the Plant Kingdom, and mammals and

290 birds in the Animal Kingdom, as well as towards temperate habitats across both kingdoms<sup>55,56</sup>.  
291 Moreover, only a rather small number of animal species currently have a sufficiently long time-  
292 series of demographic models to be included in our analytical pipeline, given our strict selection  
293 criteria (see Methods). Filling the demographic gap across continental scales, particularly South  
294 America and Africa, remains a pressing issue to gain a holistic understand of how natural  
295 populations respond to environmental stochasticity<sup>55,56</sup>. High-resolution demographic data,  
296 however, take by definition a long time to be produced, which makes filling this gap an enduring  
297 commitment by population ecologists in the coming decades.

298 Ecology and conservation biology will improve the ecological forecasting of population  
299 responses to environmental conditions by considering a more flexible life history axis that  
300 explicitly accounts for the capacity of natural population to respond to environmental stochasticity:  
301 the *demographic buffering continuum*. Indeed, this continuum explicitly quantifies how  
302 populations respond to environmental stochasticity by evaluating their effects on long-term  
303 population viability in real environments. By developing and applying the demographic buffering  
304 continuum here, we succeeded in quantifying the effect of environmental stochasticity on  
305 population responses and linking these responses to life history traits and their evolutionary  
306 history. Mostly important, our approach allows us to show that plants and animals share  
307 commonalities in how they respond to environmental stochasticity, suggesting that distinguishing  
308 multicellular organisms by taxonomic boundaries may hinder our understanding of the responses  
309 of natural populations to environmental stochasticity<sup>57</sup>. Together, our approach and findings  
310 highlight a promising way to better parameterise population models and improve population  
311 forecasts in the Anthropocene.

312

313 **4. Materials and Methods**

314 To test our hypotheses, we developed a Bayesian Generalised Linear Mixed Model (GLMM) with  
315 and without phylogenetic corrections (see Eq. 1). Doing so allows us to test the robustness of our  
316 results to the role of shared ancestry in our comparative analyses. Having established a  
317 demographic buffering continuum of variance (Fig. 1), we then performed separate models to  
318 better understand the importance of five vital rates (survival, growth, shrinkage, reproduction, and  
319 clonality) in determining the position of species' populations along the said continuum. Briefly, to  
320 position those populations on a multivariate space and test for the existence of a demographic  
321 buffering continuum, we derived life history traits from Matrix Population Models (MPMs;<sup>58,59</sup>).  
322 To examine the role of environmental regimes on demographic buffering, we extracted  
323 environmental data from CHELSAcruts<sup>60</sup> during the period when each population was studied.  
324 Data collection, model parametrisation, and the general analytical approach are detailed below.  
325

326 *Demographic data and species responses to environmental stochasticity*

327 To assess the roles of vital rates in shaping stochastic population growth rates ( $\lambda_s$ ), we used time  
328 series of MPMs from natural populations. An MPM is a discrete-state mathematical representation  
329 of the life cycle of a species, typically represented by a matrix  $A$ . Each matrix element  $a_{ij}$  in a  $A$   
330 represents the contribution of a current (st)age to the next (st)age via survival, growth  
331 (development/progression), shrinkage/retrogression, and reproduction of individuals<sup>58,61</sup>. These  
332 MPMs can be decomposed into submatrices representing the different processes of the life cycle:  
333 the  $U$  submatrix describes survival-dependent transitions (e.g., progression, retrogression), while  
334 the  $F$  and  $C$  submatrices describe sexual and clonal reproductions, respectively<sup>59</sup>. The MPMs and  
335 their decomposed submatrices used in this study were selected from the COMPADRE Plant Matrix

336 Database v6.23.5.0<sup>32</sup>, and the COMADRE Animal Database v4.23.3.1<sup>33</sup>, which contain 792 plant  
337 species with 8,994 MPM and 429 animal species with 3,488 MPMs, respectively.

338 Population responses to environmental stochasticity were analysed by estimating the  
339 overall effect of temporal variation in vital rates on the stochastic population growth rate  $\lambda_s$ .  
340 Population responses were assessed via the well-established method of the sum of stochastic  
341 elasticities within respect to variance,  $\sum E_v^\sigma$ <sup>48,61,62</sup>. Briefly, this approach estimates the extent to  
342 which small changes in the mean and variance of a given vital rate  $v$  (or matrix element,  $a_{ij}$ ) affects  
343  $\lambda_s$ . In mathematical terms, stochastic elasticities are the partial derivative of the vital rates  $v$  (or  
344 matrix elements) ( $e_{ij}^s$ ) over the MPM time series weighted by the relative contribution to  $\lambda_s$ , and  
345 are typically expressed as  $e_{ij}^s = (a_{ij} \times \partial \lambda_s) / (\lambda_s \times \partial a_{ij})$ . The overall contribution of each vital  
346 rate  $\sum E_{ij}^s$  to  $\lambda_s$  is always 1, but said overall contribution can be partitioned into the effect of  
347 perturbing the mean ( $\mu$ ) values of vital rate  $\sum E_{ij}^\mu$  or its variance ( $\sigma$ ),  $\sum E_{ij}^\sigma$ , such that  $\sum E_{ij}^s = \sum E_{ij}^\mu$   
348  $+ \sum E_{ij}^\sigma$ . The variance component  $\sum E_{ij}^\sigma$  ranges between 0 to  $-\infty$ , where values close to zero means  
349 that vital rate temporal variation has a nearly negligible impact on  $\lambda_s$ <sup>48</sup>.

350 For illustration, consider a vital rate  $v$  tracked over time in a population. Because  
351 environmental conditions are not static, some degree of change in these vital rates may be expected  
352 between the intervals  $t \rightarrow t+1$ ,  $t+1 \rightarrow t+2$ , etc. The differences in the values  $v$  and their effect on  
353  $\lambda_s$  each time step represents the population's response to the environment during the said time  
354 interval (or due to lag effects; see<sup>63</sup>). The relative impact of each vital rate  $v$  on  $\lambda_s$  can be readily  
355 assessed by its associate deterministic elasticity value, and the cumulative sum of these stochastic  
356 elasticities with respect to the temporal variance in  $v$  can thus be interpreted as the overall  
357 demographic impact on  $\lambda_s$ <sup>61,62</sup>.

358 Importantly, while previous works have developed this approach for matrix  
359 elements<sup>34,48,62,64</sup>, here we extend the method to evaluate the effects of the underlying components  
360 of matrix elements – vital rates,  $v$  – thus offering higher resolution and allowing evaluating the  
361 impact of survival independent of other survival-dependent processes such as growth and  
362 shrinkage<sup>65</sup>. Unlike matrix elements, elasticities in the underlying vital rates might be negative<sup>65</sup>,  
363 thus the sum of stochastic elasticity of  $\lambda_s$  with respect to vital rate temporal variance for the  
364 underlying vital rates ranges from  $-\infty$  to  $+\infty$ . However, the main pattern persists, with  $\sum E_v^\sigma \approx 0$   
365 representing more demographically buffered populations, and  $|\sum E_v^\sigma| \gg 0$  representing  
366 populations where temporal variation of vital rates strongly affects  $\lambda_s$ , either negatively or  
367 positively. As such, our approach explicitly accounts for the way that a given environmental  
368 regime may impact vital rates and how these vital rates, in turn, shape the overall performance of  
369 the population<sup>61,62</sup>. In our study, vital rates were retrieved from MPMs organised into three  
370 submatrices.  $U$ ,  $F$  and  $C$ <sup>59,65</sup>. Specifically, survival, growth, and shrinkage were obtained from  
371 submatrix  $U$ , whereas sexual reproduction and clonal reproduction were estimated from the  
372 submatrices  $F$  and  $C$ , respectively. To do so, we used the family function *vr\_* (e.g., *vr\_growth*,  
373 *vr\_shrinkage*) in the *Rage* R package<sup>59</sup>. Having access to already decomposed submatrices in  
374 COMPADRE and COMADRE, we explored the proportional contribution of each vital rate (e.g.,  
375  $E_{Survival}^\sigma$ ,  $E_{Reproduction}^\sigma$ ) to  $\sum E_v^\sigma$ , represented by  $\left[ \frac{|E_v^\sigma|}{\sum |E_v^\sigma|} \right] * 100$ .

376 The variable  $\sum E_v^\sigma$  estimates population responses to environmental stochasticity by  
377 recognising multiple evolutionary and physiological processes. For instance, physiological  
378 constraints might limit variation in reproduction<sup>66</sup> as well as canalising selection<sup>67</sup>, both  
379 evolutionary processes pushing populations to the buffering end<sup>48</sup>. Meanwhile, disruptive selection  
380 and high phenotypic plasticity might support adaptative variation, thus pushing populations to less-

381 buffered end<sup>21,47</sup>. Furthermore, high values of  $|\sum E_v^\sigma|$  indicate heightened responsiveness to  
382 environmental stochasticity, regardless of whether this responsiveness is favoured by natural  
383 selection<sup>62</sup>. Despite limited inference, this approach overcomes existing approaches by: (1)  
384 considering the environmental stochasticity experienced by populations not explicitly accounted  
385 in the nonlinearity index, which is calculated from their mean MPMs<sup>22</sup>; and (2) not being affected  
386 by constrained variation existing near the extreme values of vital rates that have puzzled the  
387 correlative approaches between vital rate variance and sensitivities<sup>17,19,27</sup>.

388

389 *Demographic data selection and phylogenetic relationships*

390 To ensure comparability across and within species, we selected MPMs from COMPADRE and  
391 COMADRE that fulfilled a series of carefully planned selection criteria to ensure comparability  
392 and robust results: (1) only natural populations (e.g., no zoo data) to explicitly link vital rates to  
393 their natural environments; (2) studies containing MPMs with at least three annual contiguous  
394 censuses to capture environmental stochasticity in the vital rates; (3) irreducible, primitive, and  
395 ergodic MPMs to ensure that each MPM represents a complete life cycle<sup>68</sup>; (4) MPMs with  
396 separated  $U$ ,  $F$ , and  $C$  submatrices that allow us to disentangle the effects of vital rates on the  
397 overall population growth rate obtained from the matrix  $A$ ; (5) populations with known GPS  
398 coordinates, so we could match the environmental data during the study period (see below) to vital  
399 rate variation; and (6) MPMs whose species are present in a well-resolved phylogeny to test the  
400 role of phylogenetic inertia on demographic buffering continuum ( $H_3$ ). Finally, we removed five  
401 populations identified as outliers (see *Life history traits, life history axes, and the life history PCA*).  
402 These selection criteria yielded a total of 889 MPMs across 134 populations of 89 species, of which  
403 121 populations belonged to 78 plant species, and 13 populations to 11 animal species.

404 To account for the evolutionary history in our models, we used the phylogenetic trees  
405 available in the MOSAIC database<sup>69</sup>. The trees are continuously updated from the EOL project<sup>70</sup>  
406 and comprise most of the species available in COMPADRE and COMADRE. In them, polytomies  
407 were resolved using the *multi2di* function from *ape* R package<sup>71</sup>. Further details regarding the  
408 construction of the phylogenetic trees are found in Salguero-Gómez et al.<sup>12</sup> for plants and Healy  
409 et al.<sup>14</sup> for animals.

410

411 *Life history traits and axes of variation*

412 The position of each species' populations along the fast-slow and reproductive strategy continua  
413 was used as covariates to test  $H_{lb}$  (below). To assess the position of each of the 134 populations  
414 along these two axes, we performed principal component analyses of the six examined life history  
415 traits. Life history traits define the timing, intensity, frequency, and duration of key demographic  
416 processes along the life cycle of any organism<sup>7,8</sup>. In life-history PCAs, life history traits are reduced  
417 to a series of dominant axes that capture the dominant combinations of life history traits and their  
418 trade-offs, thus offering a quantitative perspective on the emerging life history strategies (e.g.,<sup>72</sup>).  
419 In plants and animals, PCAs of life history traits have highlighted the existence of two dominant  
420 axes reflecting a trade-off between development and survival (the fast-slow continuum<sup>73,74</sup>, and  
421 the different reproduction strategies, from semelparous to extremely iteroparous (the reproductive  
422 strategies continuum<sup>74</sup>.

423 Here, we derived the following six key life history traits from our examined MPMs: (1)  
424 individual development ( $\gamma$ ); (2) mean life expectancy ( $\eta_e$ ), (3) distribution of mortality risk along  
425 the life cycle ( $P$ ); (4) probability of achieving reproduction before dying ( $p_a$ ); (5) mean age at first  
426 reproduction ( $L_a$ ); and (6) reproductive window ( $L$ ). The combination of these six life history traits

427 in populations of animals or plants adequately defines their life history strategies via multivariate  
428 analyses such as principal component analyses (PCA<sup>12,14,73</sup>). Once the life history traits were  
429 derived, we ensured a robust implementation of the PCA by removing outlier populations based  
430 on the Mahalanobis distance using the *maha* function from the *rstatix* R  
431 package<sup>75</sup>. Briefly, this approach calculates the distance of each species population from the centre  
432 of the multivariate distribution and removes those populations whose distance is greater than  
433 expected by chance, assuming a 99% C.I (Table S2).

434 We performed a PCA using the *prcomp* function from the *base* R package. We retained the  
435 first two principal components (PC) because they together captured a similar amount of variation  
436 to that achieved by recent studies used to define the fast-slow and reproductive strategy  
437 continua<sup>14,74</sup>. Together, these  $PC_{1LH}$  (life history PC1) and  $PC_{2LH}$  explained 66.4% of the  
438 variation in life history traits ( $PC_{1LH}$ : 38.0%;  $PC_{2LH}$ : 28.4%; Figure S1). To quantify the position  
439 of each population in the two-dimensional space defined by  $PC_{1LH}$  and  $PC_{2LH}$ , we obtained the  
440 PCA scores with the function *scores* of the *Vegan* R package v2.5.7<sup>76</sup>.

441  
442 *Environmental data, environmental stochasticity, and the environmental PCA*  
443 To test  $H_3$ , if higher stochasticity in environmental variables pushes less buffered responses, we  
444 linked demographic responses to environmental stochasticity. We started by quantifying the  
445 environmental stochasticity experienced by our 134 examined populations, and extracted  
446 environmental information from CHELSAcruts<sup>60</sup>. To do so, we downloaded 1 km<sup>2</sup> gridded  
447 monthly values of maximum and minimum temperature and total monthly precipitation that  
448 corresponded to latitude and longitude, as well as the years of each study selected from  
449 COMPADRE and COMADRE. The CHELSAcruts database includes climatic information from

450 1901 to 2016, thus including the temporal extent of all populations used in this study (earliest start  
451 in 1938 and latest end in 2011; See supplementary material).

452 Because we are interested in demographic responses to environmental stochasticity rather  
453 than mean temperature or precipitation, we decomposed each climatic variable  $Y$  into three groups  
454 of variables that represent trend ( $T$ ), seasonality ( $S$ ), and stochasticity ( $R$ ). We derived these  
455 variables using a seasonal decomposition through an additive moving averages model toward the  
456 *decompose* function in the *base* R package<sup>77</sup>. Briefly, this function computes the trend component  
457 of the variable of interest (e.g., monthly temperature) using an additive moving average approach.  
458 This trend is then subtracted from the time series. The resulting time series represents the periodic  
459 fluctuation - the seasonality component ( $S$ ). Finally, trend and season are discounted from the raw  
460 time series and the residuals represent the stochasticity of the environmental component -  $R$ <sup>77</sup>. For  
461 each component of time series  $Y$  (i.e.,  $T_Y, S_Y, R_Y$ ), this approach allow us to derivate the mean  
462 ( $\bar{T}_Y, \bar{S}_Y, \bar{R}_Y$ ), relative amplitude ( $\frac{\max-\min}{\text{mean}}$ ;  $\Delta T_Y, \Delta S_Y, \Delta R_Y$ ), and coefficient of variation (relative  
463 stochasticity hereafter,  $T_Y^{CV}, S_Y^{CV}, R_Y^{CV}$ ). However, we only retained those variables strictly related  
464 to change in mean-variance environment and with direct biological or climate meaning. Thus, only  
465 the mean trend of the environmental conditions ( $\bar{T}_Y$ ), amplitude of trend component ( $\Delta T_Y$ ) and the  
466 relative stochasticity of the random component ( $R_Y^{CV}$ ). While the later component represents the  
467 monthly environmental uncertainty, the other environmental variables represent how environment  
468 has changed during the study time compared to the mean conditions.

469 Similar to the life history PCA described above, we also applied a PCA to environmental  
470 data (Environmental PCA,  $PC_{Env}$  hereafter) to retain those variables that best describe variation in  
471 environmental conditions across our 134 populations. Before performing the PCA, we assessed  
472 the collinearity of the environmental variables by reducing the highly correlated ( $|\rho| > 0.8$  as the

473 threshold; Figure S2). As such, only the following six variables were further examined through  
474 our environmental PCA: (1) Mean value of the maximum temperature trend ( $\bar{T}_{TempMax}$ ), (2)  
475 relative stochasticity of maximum temperature ( $R_{TempMax}^{CV}$ ), (3) relative amplitude of the trend of  
476 the maximum temperature ( $\Delta T_{TempMax}$ ), (4) relative amplitude of the trend of the minimum  
477 temperature ( $\Delta T_{TempMin}$ ), (5) mean value of the precipitation trend ( $\bar{T}_{Prec}$ ), and (6) relative  
478 amplitude of the trend of the maximum temperature ( $\Delta T_{Prec}$ ). The first two PCs emerging from  
479 this next step explained 50.9% of the variation in environmental stochasticity separating those  
480 populations from lower to higher stochastic environments (Figure S2). Principal component axis  
481 1 ( $PC1_{Env}$ ) explains 30.6% of the variation, and describes relative monthly stochasticity in  
482 temperature,  $R_{MaxTemp}^{CV}$ , with a gradient from the tropical region to higher latitudes (Figure S3). In  
483 contrast,  $PC2_{Env}$ , which explains 20.3% of the environmental variation, describes differences in  
484 the amplitude of trend in precipitation,  $\Delta T_{Precipitation}$ .  $PC2_{Env}$  is higher in more arid places such  
485 as deserts and the Mediterranean region. Therefore, we refer to these environmental axes as  
486 temperature stochasticity ( $PC1_{Env}$ ) and seasonal aridity ( $PC2_{Env}$ ).

487

#### 488 *Statistical analysis and the phylogenetic component*

489 Hypotheses  $H_{lb}$ ,  $H_2$  and  $H_3$  were assessed using a single mathematical model (Equation 1) where  
490 competing explanatory variables representing life history ( $PC_{LH}$ ) and environmental stochasticity  
491 ( $PC_{Env}$ ) were used to explain sum of stochastic elasticities with respect to the variance,  $\sum E_v^\sigma$ .

$$492 \quad \sum E_v^\sigma = \alpha + \beta_{PC1_{LH}} * \beta_{PC2_{LH}} + \beta_{PC1_{Env}} * \beta_{PC2_{Env}} \quad (\text{Eq. 1})$$

493 Equation 1 assumes that the capacity of a population to buffer against to environmental  
494 stochasticity,  $\sum E_v^\sigma$ , can be predicted by the position of the populations within the two main axes  
495 of life histories ( $\beta_{PC1_{LH}}$ = fast-slow continuum,  $\beta_{PC2_{LH}}$ = degree of iteroparity; Fig. 1A) and the

496 environmental conditions that the populations faced during the study time ( $\beta_{PC1_{Env}}$ = temperature  
497 stochasticity,  $\beta_{PC2_{Env}}$ = Seasonal aridity; Fig. 1B), including an intercept. The life history axes  
498  $PC1_{LH}$  and  $PC2_{LH}$ , along with the environmental axes  $PC1_{Env}$  and  $PC2_{Env}$ , were  $z$ -transformed  
499 ( $\mu = 0$ , and  $sd=1$ ). This normalisation allows for the comparison among  $\beta$  estimates across all  
500 variables regarding their relative contribution to determine population's position along the  
501 demographic buffering continuum. Here, we further distinguish between  $\beta\lambda$  and  $\beta$  to refer to the  
502 slope estimates in Eq. 1 with and without phylogenetic corrections, respectively.

503 We used a Bayesian Phylogenetic Generalised linear model to estimate the most suitable  
504 contribution of each of our variables to predict the degree of demographic buffering,  $\sum E_v^\sigma$ . The  
505 Bayesian Phylogenetic Generalised linear model was performed via the *MCMCglmm* R package<sup>78</sup>,  
506 according to de Villemereuil and Nakagawa<sup>79</sup>. The GLMMs were settled with a flat prior  
507 distribution  $N(0,0.2)$  with 50,000 iterations. Finally, 95% of the posterior density distributions for  
508 each variable were compared and accepted as significant when they did not overlap 0 (fake p-value  
509 in the MCMCglmm output,<sup>78</sup>). Finally, we estimated the phylogenetic signal using the Pagel's  $\lambda$   
510 (not to be confused with [stochastic] population growth rate  $\lambda$  [ $\lambda_s$ ]), according de Villemereuil and  
511 Nakagawa<sup>79</sup>. Briefly, Pagel's  $\lambda$  ranges between 0 and 1, where values close to 0 represent complete  
512 randomness in the examined variable and values close to 1 suggest a strong influence of  
513 evolutionary history determining the state of the variable<sup>80,81</sup>.

514

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520

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689

690 **Figure legends**

691 **Figure 1.** Plant (green) and animal (blue) range along a continuum of demographic buffering  
692 against effect of temporal variation in vital rates. Said continuum is quantified by the sum of  
693 stochastic elasticities within respect to the variance  $|\sum E_v^\sigma|$  in the vital rates (*i.e.*, survival,  
694 individual-level growth, individual-level shrinkage, reproduction, and clonality). Values of  $|\sum E_v^\sigma|$   
695 represent the extent to which changes in the temporal variation of a given vital rate affect the  
696 stochastic population growth rate ( $\lambda_s$ ) in 134 natural populations (13 animals and 121 plant species)  
697 retrieved from the COMADRE (version 4.23.3.1) and COMPADRE (v. 6.23.5.0) databases. At  
698 the buffering-end of the continuum (right;  $|\sum E_v^\sigma| \sim 0$ ), vital rates either vary less or the observed  
699 variation has little to negligible effect on  $\lambda_s$ . At the not buffered end (left;  $|\sum E_v^\sigma| >> 0$ ), the observed  
700 variation on vital rates strongly shapes  $\lambda_s$  values.

701

702 **Figure 2.** For most plants and animals, the temporal variance in survival is the main driver of the  
703 responses of natural populations to environmental stochasticity, followed by individual-level  
704 growth and reproduction. **A.** The relative importance of each vital rate (elasticities,  $E_v$ ) to  
705 population growth rate,  $\lambda_s$  (Mean: circle; S.E.: bars). **B.** Stochastic elasticity of  $\lambda_s$  with respect to  
706 the vital rate temporal variance ( $E_v^\sigma$ ) of the vital rates: survival, growth, shrinkage, reproduction,  
707 and clonality. “Cumulative” refers the cumulative variance effect of all vital rates on  $\lambda_s$ ,  $\sum E_v^\sigma$ .  
708 Plants and animals are represented by different colours and shapes, with colours being subset based  
709 on taxonomic Order for animals and life-forms for plants. Overall, 134 populations of plants  
710 (n=121) and animals (n=13) were included.

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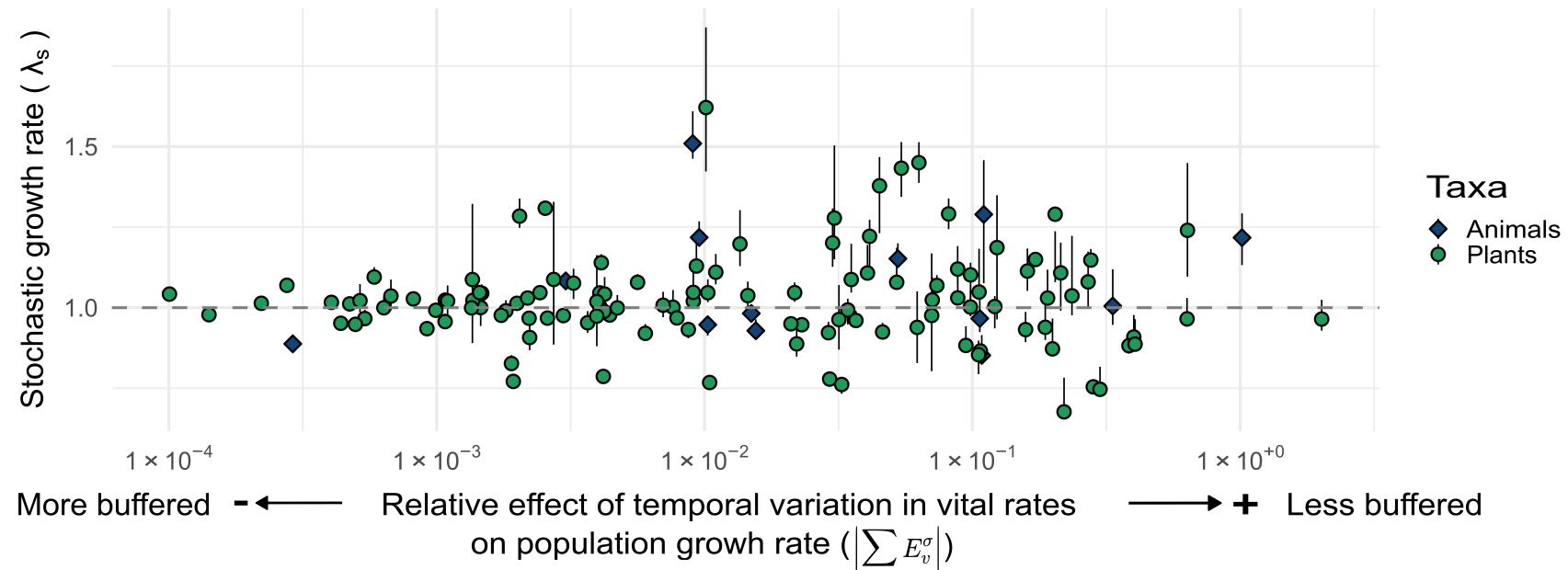
712 **Figure 3.** The importance of life history traits and environmental stochasticity on the demographic  
713 buffering capacity of natural populations depends strongly on phylogenetic relationships. **A.**  
714 Predictive power of the life history principal component (PC) axes and environmental stochasticity  
715 PC on the positioning of species' populations along the buffering continuum, measured as the  
716  $\sum E_v^\sigma$ . The shown posteriors were obtained via MCMCglmm models with (red) and without  
717 (purple) phylogenetic corrections. The fast-slow continuum and reproductive strategies continuum  
718 is represented by  $PC_{1LH}$  and  $PC_{2LH}$  (Figure S1), respectively; whereas environmental  
719 stochasticity in temperature and aridity represents the variation in the environment experienced by  
720 the examined populations as described by  $PC_{1Env}$  and  $PC_{2Env}$  (Figure S2). Significant  
721 relationships are shown in black, non-significant are blurred. **B.** Distribution of our estimates of  
722 phylogenetic signals (Pagel's  $\lambda$ ) for animals (blue) and plants (green) from our phylogenetic  
723 MCMCglmm model, evidencing the importance of phylogenetic inertia in determining how life  
724 history strategies and environmental regimes shape population responses to environmental  
725 stochasticity,  $\sum E_v^\sigma$ .

726

727 **Figure 4.** Life history traits and environmental stochasticity have variable contributions on the  
728 effects of the temporal variation in vital rates,  $v$ , on the stochastic population growth rate,  $\lambda_s$ . **A.**  
729 Predictive power of the life history principal component (PC) axes and environmental stochasticity  
730 PC on the positioning of species' populations along the demographic buffering continuum,  
731 measured as  $\sum E_v^\sigma$ . The fast-slow continuum and reproductive strategies continuum is represented  
732 by  $PC_{1LH}$  and  $PC_{2LH}$  (Figure S1), respectively; whereas environmental stochasticity in  
733 temperature and aridity represents the variation in the environment experienced by the examined  
734 populations as described by  $PC_{1Env}$  and  $PC_{2Env}$  (Figure S2). **B.** Distribution of our estimates of

735 phylogenetic signals (Pagel's  $\lambda$ ) for animals (blue) and plants (green) from our phylogenetic  
736 MCMCglmm model, evidencing a variable importance of phylogenetic inertia in determining how  
737 life history strategies and environmental regimes shape population responses to stochasticity,  
738  $\sum E_v^\sigma$ .

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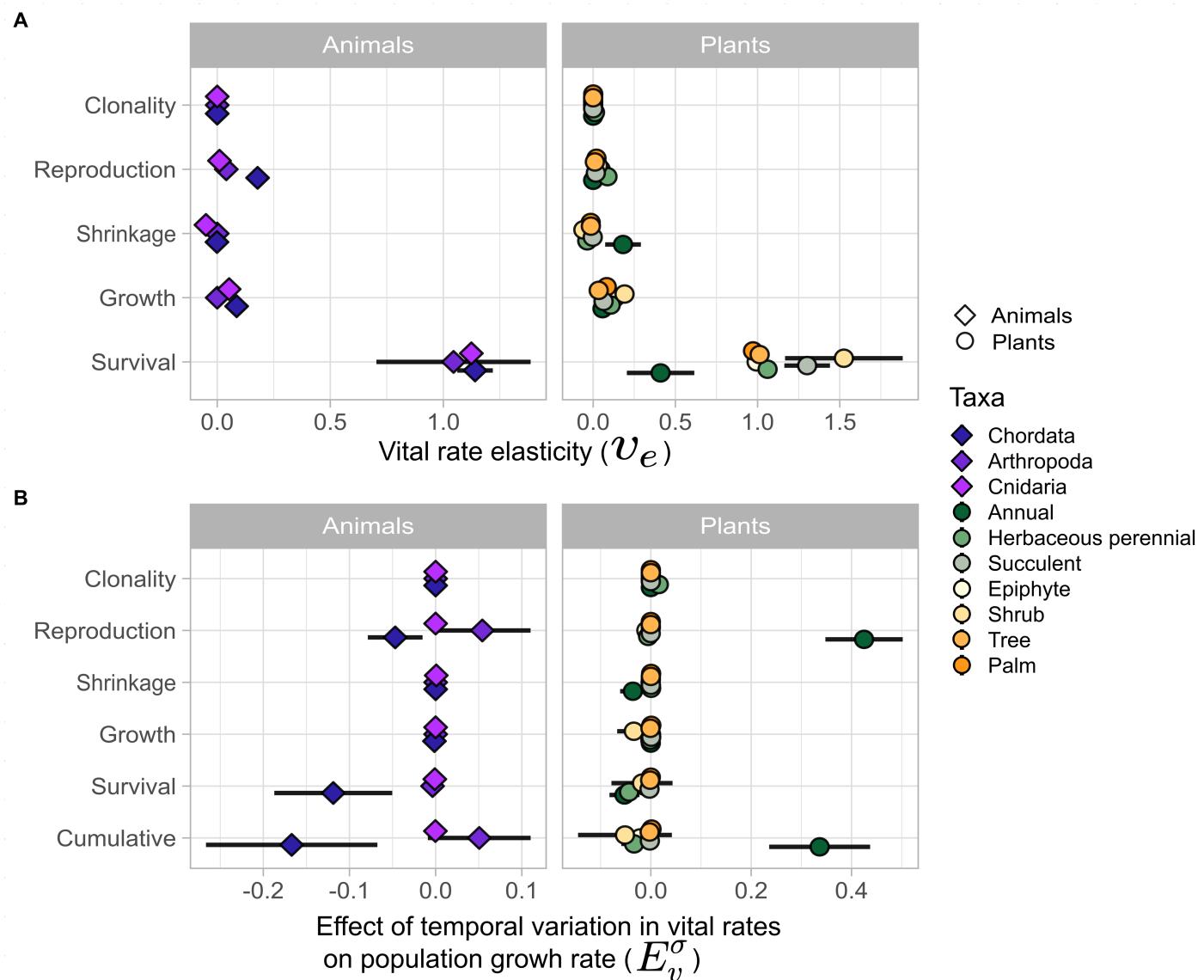
**Figure 1**

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744 **Figure 2**



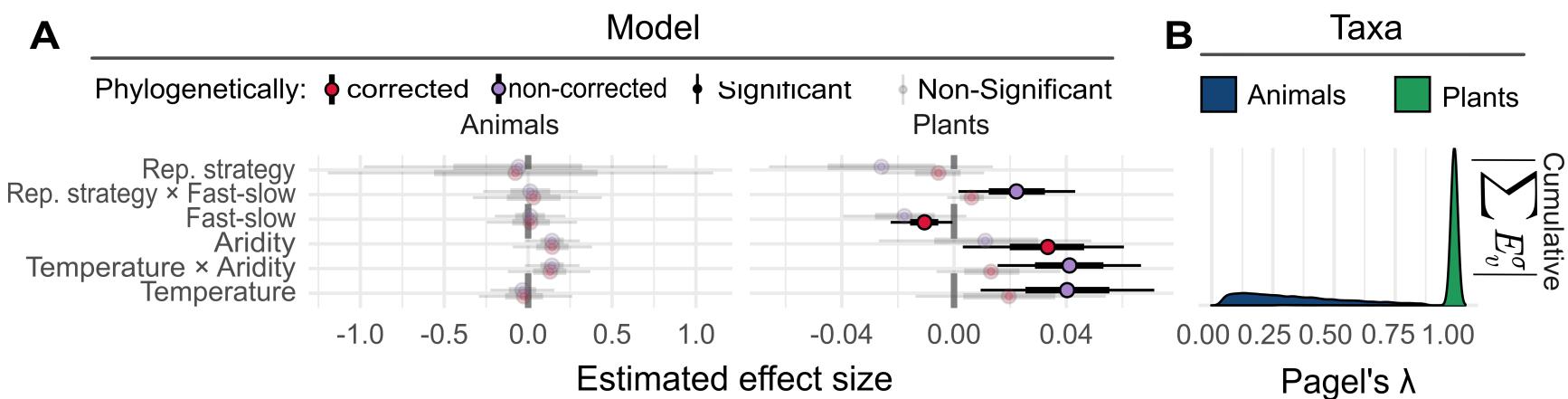
746 **Figure 3**

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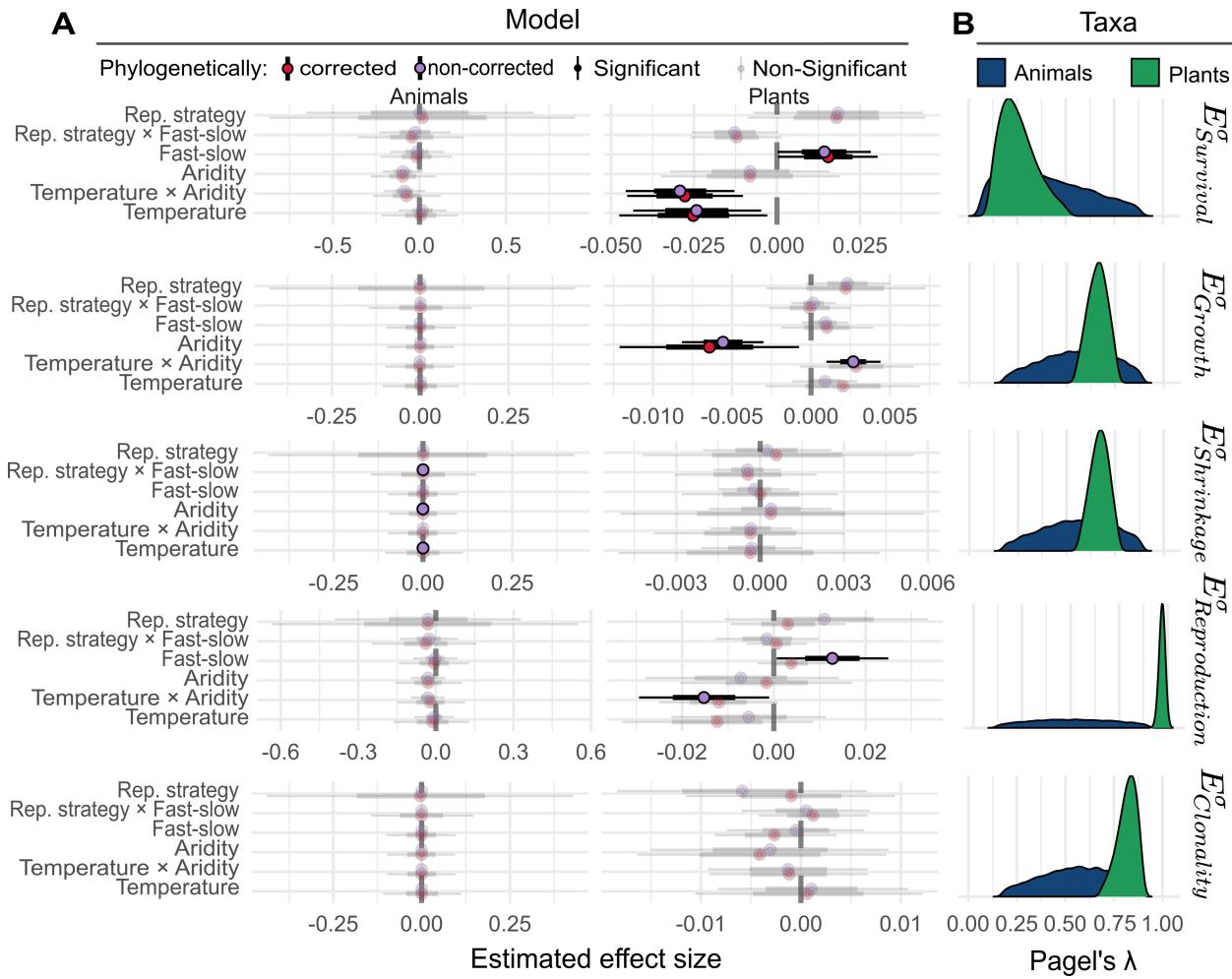


751 **Figure 4**

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