Life-history dynamics: damping time, demographic dispersion and generation time

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12 Abstract

13 Transient dynamics are crucial for understanding ecological and life-history
 14 dynamics. In this study, we analyze damping time, the time taken by a pop-
 15 ulation to converge to a stable (st)age structure following a perturbation,
 16 for over 600 species of animals and plants. We expected damping time to be
 17 associated with both generation time T_c and demographic dispersion σ based
 18 on previous theoretical work. Surprisingly, we find that damping time (calcu-
 19 lated from the population projection matrix) is approximately proportional
 20 to T_c across taxa on the log-log scale, regardless of σ . The result suggests
 21 that species at the slow end of fast-slow continuum (characterized with long
 22 generation time, late maturity, low fecundity) are more vulnerable to ex-
 23 ternal disturbances as they take more time to recover compared to species
 24 with fast life-histories. The finding on damping time led us to next examine
 25 the relationship between generation time and demographic dispersion. Our
 26 result reveals that the two life-history variables are positively correlated on
 27 a log-log scale across taxa, implying long generation time promotes demo-
 28 graphic dispersion in reproductive events. Finally, we discuss our results in
 29 the context of metabolic theory and contribute to existing allometric scaling
 30 relationships.

31 Main

32 In a constant environment, (st)age-structured populations tend towards a
 33 stable demographic structure (Lotka 1939; Leslie 1945, 1948; Lefkovitch 1965;
 34 Caswell 2001). However, disturbances such as environmental fluctuations,
 35 disease, and biological invasions can alter the size or structure of a popula-
 36 tion, so understanding the response to fluctuations and resulting transient
 37 dynamics are important to many questions in ecology and evolution (Lande
 38 et al. 2003; Gamelon et al. 2014). In an era when anthropogenic activities are
 39 altering global biodiversity, reshaping populations, and even driving species

40 to extinction (Faurby and Svenning 2015) it is even more important to ask:
 41 What is the effect of external disturbances on populations? Are some species
 42 or taxa more vulnerable to perturbations than others? To help answer such
 43 questions, we analyzed the biological determinants of the damped response
 44 of populations as they recover from an external disturbance.

45 A population structure that experiences a disturbance returns towards
 46 stability in a sequence of damped cycles. The damping rate $d > 0$ mea-
 47 sures how a population responds to disturbance, by quantifying the speed at
 48 which population converges to a stable (st)age distribution. The damping
 49 time $\tau = (1/d)$ is the time scale over which the effect of a disturbance dies
 50 away. A short damping time (equivalently, a large damping rate) means that
 51 population’s structure recovers rapidly from a perturbation, and implies a
 52 short demographic memory (Caswell 2001; Keyfitz and Caswell 2005). It
 53 is well known that the period of the damped cycles is close to the cohort
 54 generation time T_c , the average age of survival-weighted reproduction (Key-
 55 fitz 1968). Biologically, the generation time T_c measures the “pace” of life
 56 (Gaillard et al. 1989).

57 Earlier work found that damping time increases with generation time T_c
 58 (Keyfitz 1968; Hughes and Tanner 2000) but decreases with the dispersion
 59 of reproductive events across the lifetime, measured by the demographic dis-
 60 persion (Coale 1972; Taylor 1979; Keyfitz 1965; Trussell et al. 1977; Wachter
 61 1991). Demographic dispersion σ is calculated as the standard deviation of
 62 survival-weighted reproduction and can be interpreted as a measure of the
 63 variation of age at reproduction around T_c . Mathematically, damping time
 64 has been shown to be approximately proportional to T_c^3/σ^2 (Keyfitz 1965;
 65 Keyfitz 1968). Consistent with these analyses, Coale (1972) found that the
 66 damping time in human populations decreases when reproduction is spread
 67 symmetrically over an increasing range of ages (i.e., with increasing σ). Tay-
 68 lor (1979) examined insect populations and found that changes in the age of
 69 first reproduction and demographic dispersion influence the damping time.
 70 Hughes and Tanner (2000) found that slow-growing corals with large T_c have

71 a longer damping time than fast-growing corals. However, these findings fo-
72 cus on groups of species (humans, insects and corals), each with a limited
73 range of generation times. Comparative studies across taxonomic groups are
74 needed to identify how damping time varies over a wide range of generation
75 times.

76 For a large collection of age-structured data on 111 diverse mammals,
77 Gamelon et al. (2014) examined metrics of transient dynamics and found
78 that short-term demographic responses to disturbance are shaped by both
79 generation time and growth rate. This study found that species characterized
80 by long generation time and low fecundity tend to decrease in population size
81 following a disturbance. They also conclude that these slow-living species
82 might be more vulnerable as they are not expected to counterbalance the
83 negative effects of disturbances by increasing population growth.

84 Here we use a more extensive dataset of plants and animals to analyse
85 transient dynamics as measured by the damping time (τ). According to the
86 approximation ($\tau \propto T_c^3/\sigma^2$), damping time is shaped by the two life history
87 measures of generation time and demographic dispersion. We expected to
88 find that damping time is proportional to the ratio T_c^3/σ^2 , in accordance
89 with theory (Keyfitz and Caswell 2005). Surprisingly, we find the simple
90 relationship that damping time is proportional to T_c across taxa on the log-
91 log scale, regardless of σ . Although the relationship is noisy, our result implies
92 that time to convergence increases with generation time. In the context of the
93 fast-slow continuum (Stearns 1983; Oli 2004; Gamelon et al. 2016), species
94 at the slow end of the spectrum (characterized with long generation time,
95 late maturity, low fecundity) are more vulnerable to external disturbances as
96 they take more time to recover compared to species with fast life-histories
97 (characterized by short generation time, high fertility, etc). This is consistent
98 with recent work that studied demographic resilience and recovery time from
99 disturbances (Capdevila et al. 2020; Lebreton et al. 2012).

100 Our result on damping time led us to examine the relationship between
101 dispersion and generation time. Previous studies find generation time to be

unrelated to dispersion (Coale 1972; Tuljapurkar et al. 2009) but are they indeed independent? Based on our first finding, we hypothesized that dispersion σ is positively correlated to generation time T_c . This hypothesis is indeed supported by our analyses, and we find that σ is proportional to T_c on a log-log scale across taxa, and the explanatory power of this correlation is high. One basis for this result is previous work that suggests life-history traits such as generation time, age of maturity, lifespan- that scale as biological units of time (same dimension as time) have similar allometric exponents (close to 0.25) (Lindstedt and Calder III 1981). This result may also suggest that counter-examples of long-lived semelparous species (e.g., some salmonids) are rare.

We close by discussing the extensions of known allometric scaling relationships between generation time, intrinsic population growth rate, and average adult body mass, M . Previous studies have shown that generation time scales with body mass as $M^{0.25}$ whereas density-independent intrinsic population growth rate scales with body mass as $M^{-0.25}$ (Charnov 1993; Brown et al. 2004). Our results imply that demographic dispersion scales with body mass in the same way as generation time. Further, our results suggest that the scaling of population growth rate with body mass holds in a wide range of environments, because the populations in our data are likely to be affected by density-dependence.

Reproduction, Dispersion and Damping

Analyses of demographic damping have focused on humans or other species that can be described using age-structure (Keyfitz and Caswell 2005; Coale 1972; Trussell et al. 1977). In age-structured populations (in a constant environment), a life history is described by age-specific survival and reproduction. At age x , the average fertility is denoted by $m(x)$ and the probability of surviving to age x by $l(x)$. The expected lifetime reproduction of a newborn is the net reproductive rate $R_0 = \sum_x l(x)m(x)$. For a cohort (individuals born

131 at the same time), the generation time is the average age of reproduction

$$T_c = \frac{\sum_x x l(x) m(x)}{R_0},$$

132 And the spread of reproduction around the mean age T_c is captured by
133 demographic dispersion σ , defined by

$$\sigma^2 = \frac{\sum_x (x - T_c)^2 l(x) m(x)}{R_0},$$

134 Similar expressions apply to stage-structured populations. In the paper by
135 Steiner et al. (2014), the expressions for T_c and σ (denoted as V_a in their
136 paper) were derived for stage-structured populations and have been used in
137 this paper. Note that none of our data sets had both stages and ages, but
138 for such cases there are appropriate formulas in Steiner et al. (2014).

139 A (st)age-structured population in discrete time is described by a popu-
140 lation projection matrix, whose dominant eigenvalue is $\lambda_0 = \exp(r_0)$ where
141 r_0 is the well-known intrinsic population growth rate. For the same matrix,
142 the leading subdominant eigenvalue is in general complex $\lambda_1 = \exp(r_1 + is_1)$
143 (where r_1, s_1 are the real and imaginary parts of the sub-dominant root re-
144 spectively and $i = \sqrt{-1}$). Here r_0 should always be larger than r_1 . These
145 eigenvalues are used to define the damping time τ and the damping rate d

$$\tau = (1/d) = \frac{1}{(r_0 - r_1)}. \quad (1)$$

146 For each case we obtain a population projection matrix from the data (about
147 which more below) and compute exactly (by standard numerical methods)
148 the corresponding eigenvalues and the damping time.

149 After a disturbance, the population structure changes as the product
150 $e^{-dt} \cos(2\pi t/T)$, with cycles of period $T \simeq T_c$ whose amplitude decreases at
151 damping rate $d > 0$. Here $d = (r_0 - r_1)$, and t is time since the disturbance.
152 Damping with $d > 0$ is assured because in general $r_0 > r_1$ for (st)age struc-

153 tured models (Caswell 2001). Thus the damping time in equation (1) is the
154 time scale of convergence to the stable (st)age distribution.

155 Our work was motivated by Wachter (1991) extending earlier work on age-
156 structured populations. He used the Lotka renewal equation to approximate
157 r_0, r_1, s_1 . For small growth rates,

$$r_0 \approx \frac{\log R_0}{T_c} + \frac{\sigma^2 (\log R_0)^2}{2 T_c^3}, \quad (2)$$

158 whereas

$$r_1 \approx r_0 - \frac{2\pi^2 \sigma^2}{T_c^3}. \quad (3)$$

159 A similar expression for r_0 holds in stage-structured populations (Steiner
160 et al. 2014). In such cases, we conjecture that r_1 is also given by the approx-
161 imation equation (3).

162 Using these approximations in equation (1), the damping time is

$$\tau = (1/d) = \frac{1}{(r_0 - r_1)} \simeq \frac{T_c^3}{2\pi^2 \sigma^2}. \quad (4)$$

163 Hence we expect that damping time τ should increase with generation
164 time T_c , and decrease with increasing age dispersion σ of reproduction.

165 Results

166 Damping time and generation time

167 From equation (4) we expect that damping time (calculated from the pop-
168 ulation projection matrix) should increase with both generation time and
169 demographic dispersion. However, we find that damping time is positively
170 correlated with generation time across 664 species of animals and plants (on
171 a logarithmic scale, see Fig 1), regardless of demographic dispersion. The
172 relationship is significant but noisy, more so for stage-based population mod-
173 els than age-based ones. The variability around the main correlation that is

174 evident in Fig 1 may have several sources:

- 175 a. the expression (4) is an approximation so higher moments of the distri-
176 bution of reproduction may be significant for some species, especially
177 those with stage-based dynamics;
- 178 b. the data reflects sampling variability, especially for populations with
179 small population size in study, and so some variation is to be expected;
- 180 c. in some populations that have long-lived stage(s), such as trees, the
181 numbers of deaths to large individuals observed during the study period
182 may be small so the corresponding estimated survival rates may be
183 artificially high.

184 Even so, Fig 1 clearly supports the conclusion that species with short
185 generation time can recover rapidly from environmental disturbances and
186 are less vulnerable to such perturbations. On the other hand, species with
187 long generation time are more vulnerable as they take longer to converge
188 to their stable (st)age demographic distribution. Across species we find a
189 scaling relationship

$$\tau \propto T_c^b, \text{ with } b \text{ between } 0.52 \text{ and } 0.66. \quad (5)$$

190 Drilling down, we asked if a similar relationship between damping time
191 and generation time hold for the species within biological classes? We found
192 a positive relationship to hold within most classes, though the variability
193 is large (see Appendix figures B.1 and B.2). The relationship is stronger in
194 classes that contain a large number of species in our data, such as *Actinoptery-*
195 *gii*, *Aves*, *Mammalia*, and *Reptilia* in animals and *Magnoliopsida* and *Liliop-*
196 *sida* in plants.

Figure 1: Damping time (τ) versus generation time (T_c) on a log-log scale for animals (*left* panel) and plants (*right* panel). The colors correspond to data as in the previous figure. The top left of each panel presents the fitted model, its coefficient of determination (R^2) and P-value based on linear regression. The standard error of the regression slope is 0.019 (left panel) and 0.017 (right panel). The damping time (τ) used is calculated exactly from each population projection matrix. The regression slopes for each dataset are: Comadre_Age (0.81), Comadre_Stage (0.72), Compadre_Stage (0.52) and GO_Age (0.76).

197 Generation time and demographic dispersion

198 Based on the first result, we hypothesize T_c is proportional to σ given the
 199 approximation (See equation (4)). Our hypothesis is supported as the result
 200 indicates generation time and dispersion to be positively related, evidenced
 201 by the remarkable linear correlation (on a logarithmic scale, see Fig 2) be-
 202 tween the two. The relationship between T_c and σ is statistically significant

203 and the degree of explanation is high with an R^2 statistic of 0.95. The regres-
 204 sion slope of $\log(\sigma)$ versus $\log(T_c)$ is close to 1 for a wide range of taxonomic
 205 groups in both plants and animals. Hence we find a scaling relationship:

$$\sigma \propto T_c^a, \text{ with } 1.12 \leq a \leq 1.16. \quad (6)$$

206 To analyze this scaling in more detail, we grouped species by biological
 207 classes, and within each class found a strong positive (logarithmic) relation-
 208 ship between demographic dispersion and generation time that contain a
 209 large number of species in our data. These classes include *Actinopterygii*,
 210 *Aves*, *Mammalia*, and *Reptilia* in animals and *Magnoliopsida*, *Phaeophyceae*
 211 and *Liliopsida* in plants. The regression slope between $\log T_c$ and $\log \sigma$ for
 212 each Class varied but were approximately close to 1 (see Appendix figures
 213 B.3 and B.4).

214 At the opposite extreme of biological detail, we can argue that in an age-
 215 structured population an increase in demographic dispersion σ likely implies
 216 a larger reproductive span as measured by the difference between age at last
 217 reproduction ω and age at first reproduction α . Based on our result for σ ,
 218 a simple hypothesis is that reproductive span $(\omega - \alpha)$ also increases with
 219 generation time, and indeed we found such a positive relationship, although
 220 noisier (see Appendix figure B.5).

Figure 2: Demographic dispersion (σ) versus generation time (T_c) on a log-log scale for animals (*left* panel) and plants (*right* panel). Age-structured animal data from Comadre (*left*, red), stage-structured animal data from Comadre (*left*, grass green), age-structured mammal data from GO (*left*, purple) and stage-structured plant data from Compadre (*right*, lake blue). The top left of each panel presents the fitted model, its coefficient of determination (R^2) and P-value based on linear regression. The standard error of the regression slope is 0.007 (left panel) and 0.006 (right panel). The regression slopes for each dataset are: Comadre_Age (1.20), Comadre_Stage (1.11), Compadre_Stage (1.16) and GO_Age (0.93).

221 Allometric scaling of life history measures with body 222 mass

223 We extend our results through allometric scaling relationships as life-history
224 variables such as- age of first reproduction, longevity, adult mortality, gener-
225 ation time and maximum intrinsic population growth rate, have been shown

226 to scale with average adult body mass (Blueweiss et al. 1978; Read and Har-
 227 vey 1989; Promislow and Harvey 1990; Gillooly et al. 2002; Brown et al.
 228 2004; Hamilton et al. 2011; Hatton et al. 2019). An immediate consequence
 229 of our results is that any allometric scaling for T_c must imply a corresponding
 230 scaling for σ and τ .

Empirically, the generation time, T_c , scales with average adult body mass M (Millar and Zammuto 1983; Gillooly et al. 2002; Brown et al. 2004; Hamilton et al. 2011; Brown et al. 2018), as

$$T_c \propto M^{0.25}.$$

231 Using the above scaling in equation (6) with $a \simeq 1$ we find:

$$\sigma \propto M^{0.25}. \quad (7)$$

232 From equation (4), the damping time scales approximately as

$$\tau \propto M^{0.25}. \quad (8)$$

233 Next use equation (6) but with $a \simeq 1$ in the growth rate equation (2) to
 234 find

$$r_0 \approx \frac{\log R_0}{T_c} + \frac{(\log R_0)^2}{2 T_c}. \quad (9)$$

235 The net reproductive rate, R_0 , is not expected to vary with average
 236 adult body mass M , based on theoretical arguments of Brown et al. (2018),
 237 Charnov (1993), and Pianka (1988), and empirical studies in the absence
 238 of density-dependent feedbacks (Charnov et al. 2007; Ginzburg et al. 2010).
 239 Even supposing that R_0 has an allometric dependence on M , the quantity
 240 $\log R_0$ in equation (9) would vary with $\log M$ and slowly with M . Given
 241 such a weak dependence, equation (9) implies that the relationship between
 242 r_0 and M is mainly due to $(1/T_c)$, and hence

$$r_0 \propto M^{-0.25}. \quad (10)$$

243 This scaling was previously known for growth rate without density-dependence
 244 (Hennemann 1983; McMahon and Bonner 1983; Charnov 1993) (i.e., for the
 245 maximum intrinsic population growth rate). In general, empirical data to
 246 estimate r_0 is collected across a wide range of density conditions. Given the
 247 diversity of environmental contexts, we did not expect observed r_0 to dis-
 248 play the above allometric relationship. However, we think large number of
 249 matrices in our dataset may offset the effect of density conditions.

250 Discussion

251 Even though not all populations converge to a stable (st)age distribution in
 252 the real world, the patterns of convergence to and deviation from the sta-
 253 ble (st)age distribution can still provide useful biological information (Carey
 254 1983; Keyfitz and Caswell 2005). Our first finding reveals a robust positive
 255 relationship between damping time and generation time. We find damp-
 256 ing time (inverse of damping rate) is positively correlated with generation
 257 time on the log-log scale, regardless of demographic dispersion. This implies
 258 that species with slow life-histories (characterized with long generation time,
 259 late maturity, low fecundity) are more vulnerable to negative environmental
 260 disturbances than species with fast life-histories. This finding is supported
 261 by Capdevila et al. (2020) who have argued that the long convergence time
 262 (slow recovery rate) of the Asian elephant (*Elephas maximus*) makes them
 263 more vulnerable to continuous habitat loss than the red squirrel (*Tamiasci-*
 264 *urus hudsonicus*). Lebreton et al. (2012) also find that conservation status
 265 deteriorates with increasing generation time. Di Camillo and Cerrano (2015)
 266 documented mass mortality events in the North Adriatic sea and observed a
 267 shift of the benthic assemblage from slow-growing and long-lived species (of
 268 the sponge *C. reniformis*) to a community dominated by fast-growing and
 269 short-lived cnidarians. Previous studies on Amazonian mammals (Bodmer
 270 et al. 1997), and birds (Owens and Bennett 2000) indicate that species with
 271 long generation times are more prone to the threat of extinction. Therefore,

272 generation time, which is not only a major axis of variation in life-history
273 tactics in mammals (Gaillard et al. 1989), also sets the time scale for response
274 and recovery of species. Our study of recovery times from disturbances can
275 inform conservation planning (Salguero-Gómez et al. 2016).

276 Our first result led us to the finding that demographic dispersion and gen-
277 eration time are positively correlated on the log-log scale. This result implies
278 that long-lived (i.e., slow) species spread reproduction over a wider age range
279 than the converse. One possible explanation is that the large demographic
280 dispersion enables slow-lived species (characterized by low fecundity) to in-
281 crease offspring survival by investing more energy in each reproductive event.
282 Also, species with slow life histories may take a long time to reach the repro-
283 ductive window, and so experience large variability during their development
284 (e.g. differences in resource utilization, growth in body size). Such variability
285 has a modest effect on fitness in long-lived populations (Tuljapurkar 1982),
286 and can ride out fluctuations by averaging over several ages (Sæther et al.
287 2013). In addition, previous theoretical arguments (Tuljapurkar 1982) have
288 shown that fitness as defined by stochastic growth rate depends on intrinsic
289 growth rate r_0 which is a function of σ and T_c (Wachter 1991). Therefore,
290 our result on the correlation between σ and T_c has implications for stochastic
291 growth rate and population dynamics in fluctuating environments.

292 Our results also suggest several allometric scaling relationships between
293 average body mass and the life history parameters of demographic dispersion,
294 damping time, and intrinsic population growth rate. The allometric scaling
295 of dispersion we found contributes to previous work that suggests life-history
296 traits that scale as biological units of time have similar allometric exponents
297 (close to 0.25) (Lindstedt and Calder III 1981). Our result on growth rate
298 also extends the previously established metabolic scaling from a density-
299 independent scenario (Charnov 1993) to a wide range of environments. The
300 metabolic theory of ecology (West et al. 1997, 1999; Brown et al. 2004)
301 may explain such empirical observations in terms of basic biological and
302 physiological processes.

303 There are limitations in our study that call for future research. Consider-
 304 ing our dataset spans a wide range of species, we did not analyse phylogenetic
 305 relationship between species which may provide scope for further work. Our
 306 analyses use the theory of density-independent time-invariant population pro-
 307 jection models, whereas research that takes density-dependence and stochas-
 308 ticity into account is needed to provide a more comprehensive picture of
 309 life-history and transient dynamics. We only consider recovery from a single
 310 disturbance event and have not studied the effects of disturbances of vary-
 311 ing magnitude or duration that may impact populations through different
 312 mechanisms (Owens and Bennett 2000). Our arguments about life-history
 313 strategies and the slow-fast continuum focus on animals (largely mammals).
 314 For plants, we need a better understanding of their life-histories to explain
 315 our findings. A deeper understanding of the deviations we observe in our
 316 results may require a more searching analysis of individual life-histories.

317 Data

318 Our aim is to examine damping time for a large number of species covering
 319 a wide range of generation time. To do so we used three databases which
 320 provide population projection matrices: COMPADRE (v.6.20.5.0) for plants
 321 (Salguero-Gómez et al. 2016); COMADRE (v.4.20.5.0) for animals (Salguero-
 322 Gómez et al. 2016); and compiled lifetables for mammals by Jean-Michel
 323 Gaillard (Gaillard et al. 2005) and Madan Oli (Oli 2004) (hereafter GO).

324 After data checking and cleaning (details in the Appendix), we have 3622
 325 matrices (664 different species) in total: in COMPADRE there are 2353
 326 stage-structured matrices (331 species); in COMADRE, there are 1029 stage-
 327 structured matrices (217 species) and 96 age-structured matrices (32 species).
 328 In the GO dataset, there are 144 age-structured matrices (112 species) after
 329 removing the matrices that were also present in COMADRE dataset.

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471 Appendix

472 A Supplementary Information on Data

473 For COMPADRE (v.6.20.5.0) and COMADRE (v.4.20.5.0) database, there
 474 were initially 8925 matrices (759 species) and 2275 matrices (415 species),
 475 respectively. Then we conducted a series of data cleaning to prepare the
 476 dataset for the analysis.

477 A.1 Data classification for age- and stage-structured 478 matrices

479 The database consists of three criteria to indicate whether the population pro-
480 jection matrix contains (st)ages based on size (MatrixCriteriaSize), develop-
481 ment (MatrixCriteriaOntogeny), age (MatrixCriteriaAge). For COMADRE
482 and COMPADRE, we first take out "NA"s in these three criteria, then use
483 them to get a rough classification of age and stage-structured data: if Ma-
484 trixCriteriaSize == "No" & MatrixCriteriaAge == "Yes" & MatrixCrite-
485 riaOntogeny == "No", it's considered as age-structured data, otherwise it's
486 stage-structured data.

487 For COMPADRE, we only consider stage- structured data for the anal-
488 ysis. For age-structured data in COMADRE, we further check the the in-
489 tersection of last row and last column in the survival matrix. If the value
490 is zero, then we classify it as a age-structured data; if it is non-zero, then
491 classify it as stage-structured data considering the population is alive in the
492 last stage observed.

493 A.2 Filters used before calculation

494 Using the flags in the dataset, we exclude data with missing values in vi-
495 tal rates (i.e, to ensure no NA's in the matrices); ensure the ergodicity of
496 population projection matrix; ensure the survival for a given age/stage is al-
497 ways less than or equal to 1; ensure the fecundity was measured in the study;
498 eliminate those matrices with non-zero cloning data; keep matrices where the
499 projection interval is non-zero; remove data from one unclear source (Master
500 thesis) with no title and author name.

501 We also remove semelparous species *Oncorhynchus tshawytscha* (Chinook
502 salmon); ensure the fertility matrix has elements only on the first row and
503 the rest of the rows are all 0; remove data with males and females vital
504 rates separately in the same population projection matrix; remove Bacteria
505 (*Spirochaetes*) and Virus (*lentivirus*); remove data with the intersection of

506 last row and last column of survival matrix equals to 1.

507 For age-structured data in COMADRE, we further ensure survival matrix
508 should only have non-zero value in sub-diagonal; ensure that the fertility
509 matrix has more than 1 non-zero value in the first row.

510 **A.3 Filters used during and after calculation**

511 For stage-structured data in both COMADRE and COMPADRE, we remove
512 matrices where $(I-U)$ inverse does not exist (where I is the Identity matrix
513 and U is the survival matrix) to enable the calculation. It should be noted
514 that we standardized the databases so that the projection interval is the
515 same (1 year) for all species. Besides, considering the biological realism, we
516 removed unlikely values by ensuring $\log(T_c) < 5$, $\log(\sigma) > -15$, and
517 $\log(\tau) < 15$.

518 B Figure

Figure B.1: Class-wise plots for damping time (τ) versus generation time (T_c) on a log scale for animals. Each panel corresponds to a Class. On the top left of each panel, we also present the fitted model and its coefficient of determination (R^2) based on linear regression. It should be noted that the damping time (τ) presented here is the exact value calculated from population projection matrix instead of the approximation in equation (4).

Figure B.2: Class-wise plots for damping time (τ) versus generation time (T_c) on a log scale for plants. Each panel corresponds to a Class. On the top left of each panel, we also present the fitted model and its coefficient of determination (R^2) based on linear regression. It should be noted that the damping time (τ) presented here is the exact value calculated from population projection matrix instead of the approximation in equation (4).

Figure B.3: Class-wise plots for demographic dispersion (σ) versus generation time (T_c) on a log scale for animals. Each panel corresponds to a Class. On the top left of each panel, we also present the fitted model and its coefficient of determination (R^2) based on linear regression.

Figure B.4: Class-wise plots for demographic dispersion σ versus generation time T_c on a log scale for plants. Each panel corresponds to a Class. On the top left of each panel, we also present the fitted model and its coefficient of determination (R^2) based on linear regression.

Figure B.5: Reproductive span ($\omega - \alpha$) versus generation time (T_c) on a log scale for age-structured animals. Different colors indicate different biological Classes. On the top left, we also present the fitted model and its coefficient of determination (R^2) based on linear regression.