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Senescence: Still an Unsolved Problem of Biology

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4

5 **Abstract**

6 Peter Medawar's 'An Unsolved Problem of Biology'¹ was one of several formal attempts to
7 provide an explanation for the evolution of senescence, the increasing risk of mortality and
8 decline in reproduction with age after achieving maturity. Despite *ca.* seven decades of
9 theoretical elaboration aiming to explain the problem since Medawar first outlined it, we
10 argue that this fundamental problem of biology remains unsolved. Here, we utilise
11 demographic information^{2,3} for 308 multicellular species to derive age-based trajectories of
12 mortality and reproduction that provide evidence against the predictions of the classical, still
13 prevailing, theories of ageing^{1,4,5,6}. These theories predict the inescapability of senescence^{1,4},
14 or its universality at least among species with a clear germ-soma barrier^{5,6}. The patterns of
15 senescence in animals and plants that we report contradict both of these predictions. With the
16 largest ageing comparative dataset of these characteristics to date, we build on recent
17 evidence^{7,8} to show that senescence is not the rule, and highlight the discrepancy between
18 existing evidence and theory^{7,8,9}. We also show that species' age patterns of mortality and
19 reproduction often follow divergent patterns, suggesting that organisms may display
20 senescence for one component but not the other. We propose that ageing research will benefit
21 from widening its classical theories beyond merely individual chronological age; key life
22 history traits such as size, the ecology of the organism, and kin selection, may together play a
23 hidden, yet integral role in shaping senescence outcomes.

24

25 **Main**

26 The evolution of senescence has long been explained by a collation of theories defining the
27 ‘classical evolutionary framework of ageing’. The central logic common to the theories
28 argues that the force of natural selection weakens with age^{1,4,5,6}. Selection becomes too weak
29 to oppose the accumulation of genes that negatively affect older age classes¹, or favours these
30 genes if they also have beneficial effects at earlier ages in life⁵, when the contribution
31 individuals make to future populations is assumed to be greater. Selection, therefore, should
32 favour resource investment into earlier reproduction rather than late-life maintenance⁶.
33 Ultimately, these theories predict, directly⁴ or indirectly^{1,5}, that senescence is inescapable⁴, or
34 at least inevitable in organisms with clear germline-soma separation^{5,6}.

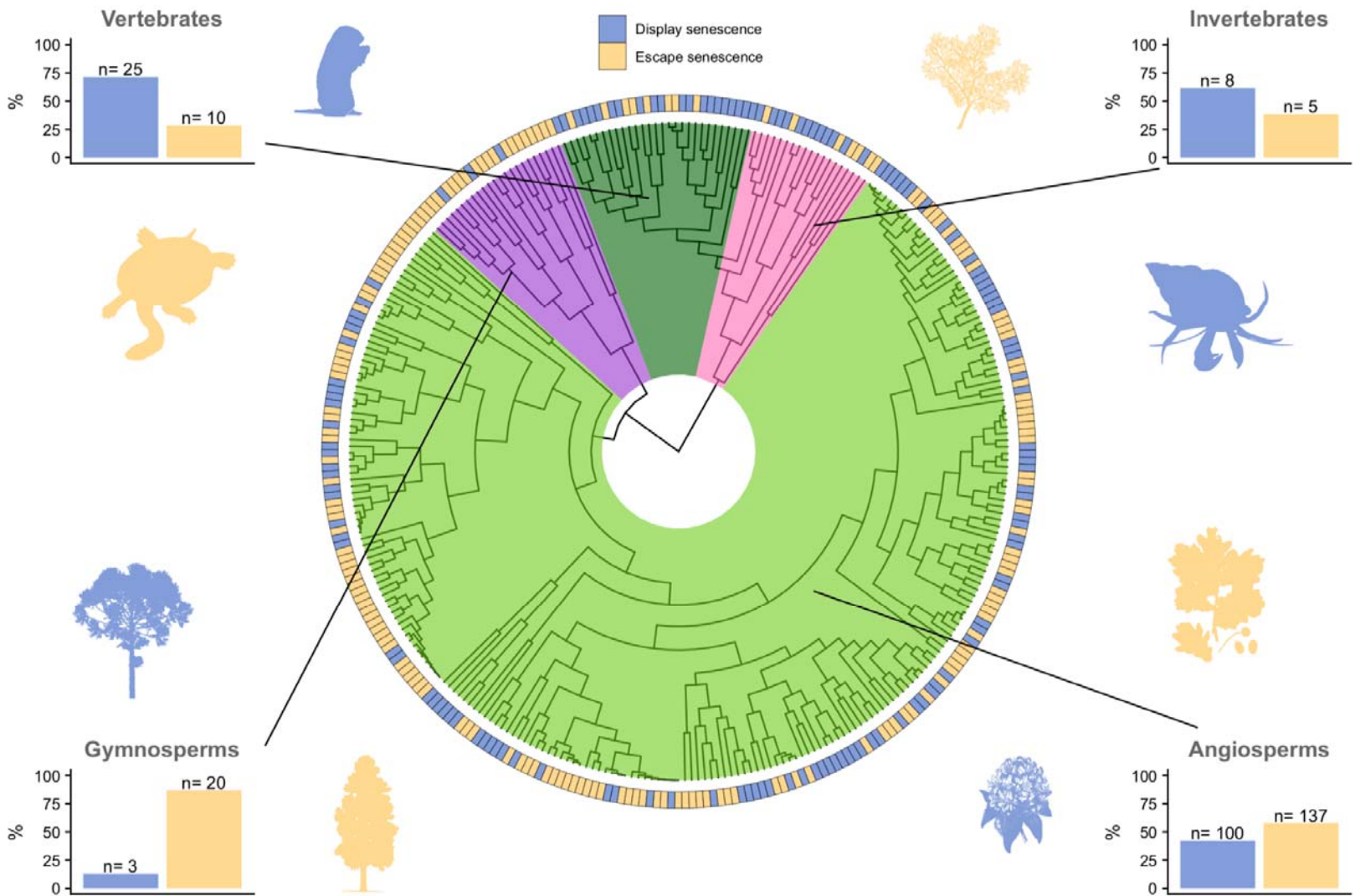
35 It takes one example to disprove any rule. Recently, a comparative description of
36 demographic patterns of ageing in 46 species of animals, plants, and algae⁸ contradicted the
37 predictions of the classical evolutionary framework. Many of the examined species displayed
38 negligible¹⁰ or even negative¹¹ senescence, where the risk of mortality remains constant or
39 decreases with age, and reproduction remains constant or increases with age. This mismatch
40 between observations and expectations have rendered the classical evolutionary framework
41 insufficient to explain the evolution of senescence across the tree of life. We now need to
42 understand mechanisms behind such variation of ageing patterns⁹, and how prevalent such
43 “exceptions” are to the rule of ageing.

44 Here, we utilise high-resolution demographic information for 48 animal² and 260
45 plant³ species worldwide to (i) provide a quantitative evaluation of the rates of actuarial
46 senescence – the progressive age-dependent increase in mortality risk with age after
47 maturation – across multicellular organisms, (ii) test whether the classical evolutionary
48 framework explains the examined diversity of senescence rates, with special attention to

49 predictions from germ-soma separation, and (iii) propose how to widen the classical
50 evolutionary framework of ageing to better encompass the tree of life.

51 First, we derived life tables¹² from a selection of species' matrix population models¹³,
52 each of which are a summary of the population dynamics of the species in question under
53 natural conditions (See Methods & Supplementary Information). We then quantified the rate
54 of actuarial senescence on the survivorship trajectory of each species' life table
55 using Keyfitz' entropy (H)¹⁴. This metric quantifies the spread and timing of mortality events
56 in a cohort as individuals age, with $H < 1$ indicating that most mortality occurs later in life
57 (*i.e.* actuarial senescence), and $H > 1$ indicating low mortality at advanced ages, whereby
58 individuals may escape actuarial senescence (See Methods & Supplementary
59 Information). Importantly, H is normalised by mean life expectancy, facilitating cross-species
60 comparison to examine general patterns and plausible mechanisms.

61



62 **Figure 1 The evolution of and escape from senescence across multicellular life.** The
63 classical evolutionary framework of ageing does not explain the evolution of actuarial
64 senescence across our 308 study species. Species that escape (yellow) and display (blue)
65 senescence, as measured by Keyfitz' entropy (H)¹⁴, are dispersed throughout the four
66 examined clades, with the percentages of each clade either displaying or escaping actuarial
67 senescence shown in the bar charts. Depicted around the phylogeny are eight representative
68 species, escaping (blue) and displaying (yellow), from each clade. Clockwise, these species
69 are *Paramuricea clavata* (Invertebrate), *Pagurus longicarpus* (Invertebrate), *Quercus rugosa*
70 (Angiosperm), *Rhododendron maximum* (Angiosperm), *Pinus lambertiana* (Gymnosperm),
71 *Taxus floridana* (Gymnosperm), *Marmota flaviventris* (Vertebrate) and *Chelodina expansa*
72 (Vertebrate).

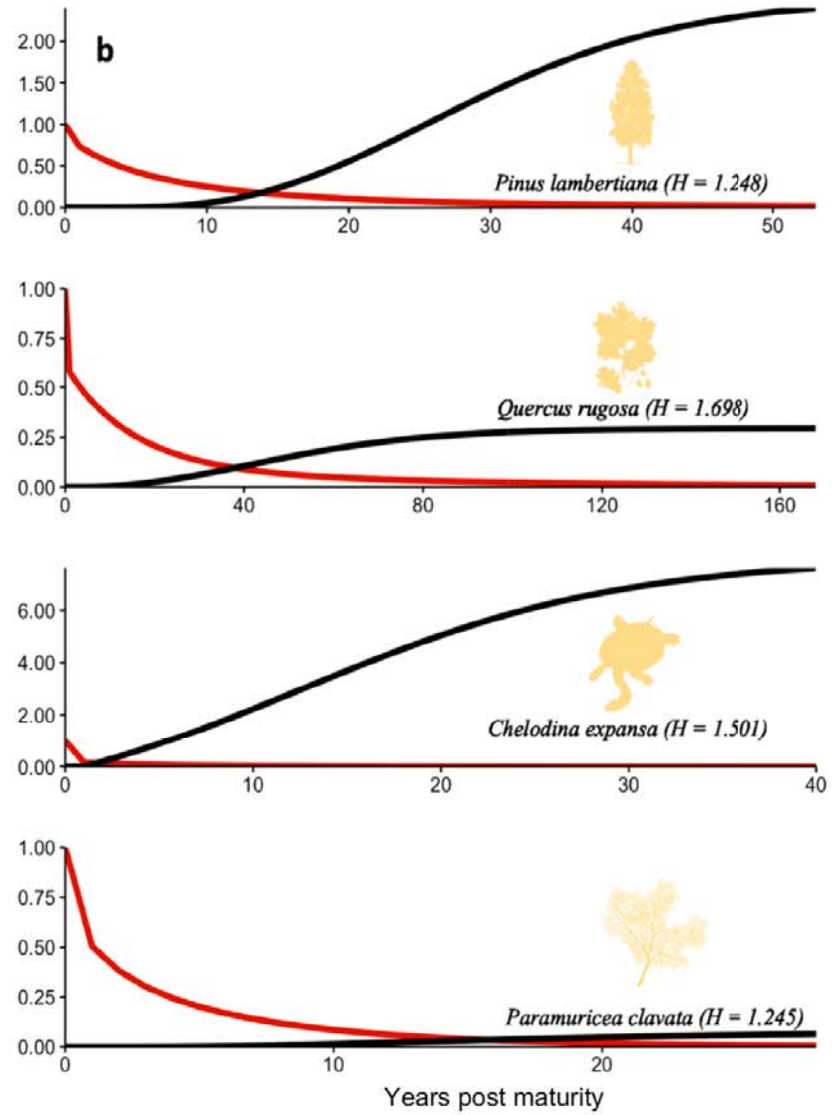
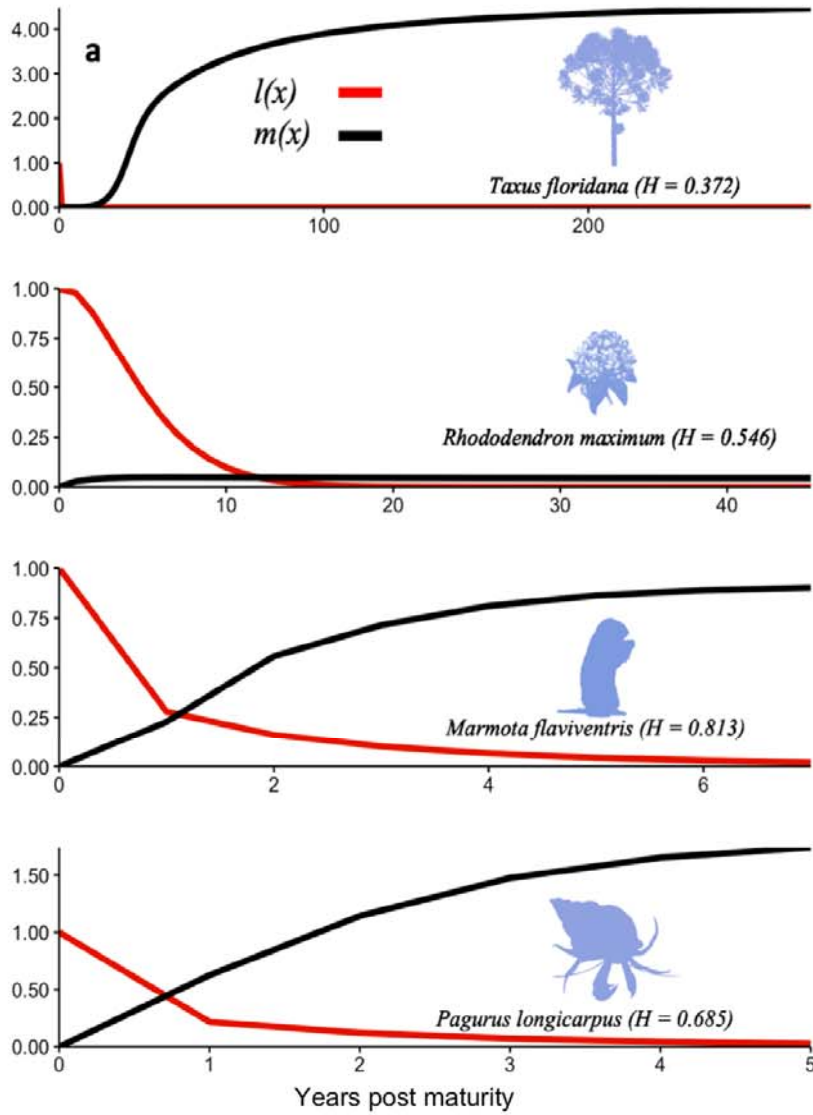
73

74 Most of the species in our analysis do not display senescence (Fig. 1, Supplementary
75 Table 1). These include approximately 30% (10/35) of the studied vertebrate species, which
76 have a clear germ-soma separation, such as the broad-shelled river turtle (*Chelodina expansa*;
77 Fig. 1). In contrast, 42% of vascular plants (angiosperms and gymnosperms), all lacking a
78 clear germ-soma barrier, display senescence (Fig. 1). In general, the evolutionary history of a
79 species in our study plays a relatively weak role in constraining its ability to escape/evolve
80 senescence. Estimates of Pagel's λ ¹⁵, a metric that measures how well phylogenetic
81 relatedness predicts the variation of a trait across species (See Methods and Supplementary
82 information) are generally weak (Extended Data Table 1), with the full analysis producing a
83 Pagel's $\lambda = 0.38$ (0.14-0.65, 95% C.I.). Overall, the emerging senescence landscape appears
84 (i) not inescapable, (ii) not inevitable in species with a germ-soma barrier, and (iii) prevalent
85 in species without a clear germ-soma barrier. These findings are in direct contradiction with
86 the predictions of the classical evolutionary framework of ageing^{1,4,5,6}.

87 The central assumption of the classical evolutionary framework of ageing, that the
88 force of natural selection weakens with age, rests on the assumption that older individuals
89 contribute less to future populations^{1,4,5,6}. This is both because fewer individuals survive to
90 later age classes¹, and individuals are expected to favour reproduction at young rather than
91 old ages^{1,5,6}. To observe how different age classes contribute to future populations in our

92 study species, we use the derived life tables¹² to quantify age-specific reproduction rates
93 ($m(x)$) for species that we previously identified to display actuarial senescence ($H < 1$) vs.
94 those that do not ($H > 1$) (See Methods & Supplementary information). The $m(x)$ trajectories
95 for all the species in our dataset can be found in Extended Data Fig. 1. For practicality, here,
96 we provide the trajectories for the eight representative species across the four clades depicted
97 in Figure 1.

98



100 **Figure 2 Age-based patterns of survivorship ($l(x)$ - red) and reproduction ($m(x)$ - black)**
101 **are often decoupled, as shown for a selected subset of the examined species in Figure 1.**
102 **a)** Species quantified as displaying actuarial senescence ($H < 1$) and **b)** species that escape
103 actuarial senescence ($H > 1$). Species are representative of vertebrates, invertebrates,
104 gymnosperms, and angiosperms. Trajectories are conditional upon reaching the age of
105 maturity, represented as 0, at which the mature cohort is defined to have entered adulthood
106 with a survivorship of 1. The trajectories of $l(x)$ and $m(x)$ run from age at maturity to the age
107 at which 5% of the mature cohort is still alive.

108

109 Classical theories of ageing predict that rates of reproduction should decline with
110 age^{1,4,5,6}. In our study species, however, patterns of $m(x)$ are diverse and appear to be
111 independent of whether the species displays or escapes actuarial senescence (Extended Data
112 Fig. 1a-h). For instance, the long-wristed hermit crab (*Pagarus longicarpus*) displays
113 actuarial senescence (Fig. 1), yet its reproduction increases with age (Fig. 2). Our results
114 suggest that an individual's risk of mortality and rate of reproduction often follow different
115 trajectories (Fig. 2, Extended Data Fig. 1a-h). For each species in our study, we only consider
116 a single studied population, and so this decoupling cannot be an artefact of intra-specific
117 variation across different populations. It follows that species may display actuarial
118 senescence, but not reproductive senescence, and *vice versa*. Thus, we urge future work to
119 consider that senescence is a two-component phenomenon of which, as displayed here, both
120 are not destined to the same fate. To fully divulge the senescence profile of a species one
121 must consider both mortality and reproduction.

122 Studies on reproductive senescence are sparser than their actuarial senescence
123 counterparts. Although, important longitudinal investigations into reproductive senescence
124 have been conducted^{16,17,18}, and current data suggest that rates of reproduction, like mortality
125 hazards, can also both increase or decrease with age. Our results support observations that
126 patterns of reproduction are variable across species (Fig. 2, Extended Data Fig. 1).
127 Developing a methodology to quantify these senescence patterns of reproduction, as done

128 here using Keyfitz' entropy¹⁴ (H) for actuarial senescence, should be a focus of future
129 theoretical work to unearth when, where, and what mechanisms drive how tightly the two
130 components of senescence co-vary.

131 In general, our results display the discrepancy between the predictions of the classical
132 evolutionary framework of ageing and empirical data. We suggest that researchers must
133 widen the framework to better encompass the biology of a more diverse range of taxa. For
134 example, the models of the classical evolutionary framework are purely age-structured, yet,
135 in some species, demographic patterns of survival and reproduction may be influenced
136 equally or even more by factors besides age¹³. Indeed, the force of selection does not always
137 decline with age for some species¹⁹. These organisms display demographic trajectories of
138 survival and reproduction that are better predicted by size rather than age, such as many
139 plants²⁰, which is supported by the 58% of studied plant species here that escape senescence,
140 or corals²¹ (e.g. *Paramuricea clavata*; Fig. 1).

141 Many of the predictions made explicit from the classical framework of ageing have,
142 until recently, long stood the test of time. Higher rates of extrinsic mortality, *i.e.* deaths due to
143 the background environment, are expected to accelerate rates of senescence, whereas juvenile
144 mortality is predicted not to play a role in the evolution of senescence⁵. Theoretical
145 advancements, however, have shown that to have a significant effect, extrinsic mortality must
146 be age-dependent²². Also, by biasing the stable age distribution of a population towards
147 younger ages, high birth rate can also reduce the strength of selection with age²³. The strength
148 of selection at a given age is dependent on both the abundance of individuals in a given age
149 class *and* the respective reproductive value of that age class^{4,23}. Following this logic, some
150 species that display senescence yet retain high reproduction at old ages (e.g. *Marmota*
151 *flaviventris* or *Pagurus longicarpus*; Fig. 1, Fig. 2) may have a stable age distribution biased
152 towards younger individuals. This outcome would render selection too weak to promote an

153 escape from senescence. Ultimately, how the environment shapes patterns of birth and deaths
154 will dictate both the reproductive value of age classes and the stable age-distribution of the
155 classes. In turn, the resulting dynamics of these pressures will affect the relative strengths of
156 age-specific selection gradients²⁴ for mortality and reproduction, and therefore patterns of
157 senescence.

158 Finally, we have only considered patterns of survival and reproduction with respect to
159 effects on the focal individual. If an individual's survival and/or reproduction affects the
160 fitness of others, however, and the interacting individuals are relatives, selection on the
161 demographic age trajectories will also be weighted by these effects²⁵. In our study, for
162 example, the killer whale (*Orcinus orca*) experiences negligible actuarial senescence ($H =$
163 0.999) (Extended Data Fig. 1a). Killer whales are an exemplar where post-reproductive
164 survival is hypothesised to have evolved due to the positive effects individuals can have on
165 the survival and reproduction of offspring, *i.e.* 'grandmother hypothesis'^{4,5,26}. This is
166 consistent with our results. Further evidence is also beginning to accrue elsewhere that
167 sociality may have an important role in driving patterns of senescence beyond the reimits of
168 'grandmothering'^{27,28}.

169 The emerging picture of senescence across multicellular organisms is at odds with the
170 widely cited predictions of the classical evolutionary framework^{1,4,5,6}. What drives the
171 evolution of senescence has attracted the attention of a vast research community, but we
172 propose that the field would benefit immensely if the attention is shifted towards the
173 underlying mechanisms allowing species to escape from senescence. We expect the greatest
174 progress to be made by researchers honing their focus to widening the classic evolutionary
175 theories to a framework not solely focused on age, but instead inclusive of the
176 aforementioned factors and with a special focus on actuarial and reproductive senescence as
177 potentially differing trajectories. Most ageing research likely stems from human desire to

178 increase human health and life span²⁹. This desire requires understanding the variation in
179 patterns of senescence across the tree of life. For now, senescence remains an unsolved
180 problem of biology.

181 **Methods**

182

183 **Data**

184 We used the COMADRE Animal Matrix Database² (v. 3.0.0) and COMPADRE Plant Matrix
185 Database³ (v. 5.0.0) to obtain age trajectories of survival and reproduction. These open-access
186 data repositories consist of matrix population models¹³ (MPMs) incorporating high-resolution
187 demographic information on the survival and reproduction patterns of over 1,000 animal and
188 plant species worldwide^{2,3}. Both databases include information on species for which the data
189 have been digitised and thoroughly error-checked. In addition, we contacted authors for
190 clarifications when any doubt about the interpretation of the life cycle of the species emerged.
191 We imposed a series of selection criteria to restrict our analyses to data of the highest quality
192 possible.

- 193 (i) MPMs were parameterised with field data from non-disturbed, unmanipulated
194 populations (*i.e.* natural populations) to best describe the species' age trajectories.
- 195 (ii) MPMs had dimension $\geq 3 \times 3$ (*i.e.* rows \times columns). Generally, low dimensions
196 MPMs lack quality for the estimation of life history traits³⁰. This selection
197 criterion also helps avoid problems with quick convergence to stationary
198 equilibrium, at which point the estimates of life history trait values and rates of
199 senescence become unreliable^{8,31}.
- 200 (iii) MPMs were only used when the entire life cycle was explicitly modelled
201 including recordings of survival, development, and reproduction for all life cycle
202 stages.

- 203 (iv) When MPMs existed for multiple populations within a given species, we
204 calculated the arithmetic element-by-element mean MPM to obtain a single MPM
205 per species.
- 206 (v) When multiple studies existed for the same species, we considered only the study
207 of greater duration to ensure the highest temporal variation in the population
208 dynamics was captured.
- 209 (vi) Studies of annual plant species modelled using seasonal projection matrices were
210 not included; we chose only species using an annual time step. This is due to the
211 difficulties of converting their population dynamics to an annual basis to compare
212 with all other species' models.
- 213 (vii) Included MPMs have stage-specific survival values ≤ 1 . In a small number of
214 published models, the stage-specific survival values can exceed 1 due to clonality
215 being hidden in the matrix, rounding errors, or other mistakes in the original
216 model^{2,3}.
- 217 (viii) MPMs were from species of which phylogenetic data was available, to ensure we
218 were able to account for phylogenetic relatedness on our models.

219 The result of these criteria was a subset of 308 species of animals and plants from the
220 initial databases, which we used for our analysis. Of these, 48 were animals, with 13
221 invertebrates and 35 vertebrates. The remaining 260 species were plants, with 23
222 gymnosperms and 237 angiosperms. We provide a list of all the species used, their
223 categorisation as displaying or escaping senescence including value of H , and their relevant
224 source study (Supplementary Table 1).

225

226 **Displaying vs escaping senescence**

227 MPMs are a summary of the population dynamics of a given species, from which we can
228 calculate several life history traits. To do so, we first must decompose an MPM (A) into its
229 sub-components¹³:

230 U – containing the stage-specific survival rates

231 F – containing the stage-specific per-capita reproduction rates

232 C – containing stage-specific per-capita clonality rates

233
$$A = U + F + C$$
 equation 1

234 This decomposition facilitates the estimation of key life history traits, including
235 Keyfitz' entropy (H)¹⁴. Calculating H requires first obtaining the age-specific survivorship
236 curve $l(x)$ from U . First, the definition of age requires a choice of a stage that corresponds to
237 “birth”. Following Jones *et al.*⁸, we defined the stage corresponding to birth as the first
238 established non-propagule stage (e.g., not seeds or seed bank in the case of plants, nor larvae
239 or propagules in animals) due to the estimate uncertainty of parameters involved in those
240 stages. The calculation of $l(x)$ was then implemented according to Caswell (p. 118-21)¹³.

241
$$l(x) = e^t U^x e^j \quad x = 0, 1, \dots$$
 equation

242 2

243 We considered survivorship trajectories beginning at the age of maturity (calculated
244 following 5.47–5.54 in Caswell¹³) and ending at the age at which 5% survivorship from
245 maturity occurs. This is because a cohort modelled by iteration of the U matrix eventually
246 decays exponentially at a rate given by the dominant eigenvalue of U , and converges to a
247 quasi-stationary distribution given by the corresponding right eigenvector \mathbf{w} . Once this
248 convergence has happened, mortality remains constant with age, and so to prevent our
249 conclusions being overly influenced by this assumption, we calculated the age at which the
250 cohort had converged to within a specified percentage (5%) of the quasi-stationary
251 distribution^{8,31}.

252 H is proportional to the area under the age-specific survivorship curve and is
253 calculated as follows

$$254 \quad H = \frac{-\log(lx)lx}{\sum lx} \quad \text{equation 3}$$

255 If most mortality occurs later in life, $H < 1$, and individuals in the population display
256 actuarial senescence. On the contrary, if $H > 1$, the risk of mortality declines with age and the
257 individuals in the population escape actuarial senescence. Here, we categorise species as
258 either escaping or displaying senescence, however, values of $H \sim 1$ are more likely to indicate
259 negligible senescence, where risk of mortality remains relatively constant with age.

260

261 **Phylogenetic analyses for actuarial senescence**

262 After categorising species as displaying ($H < 1$) or escaping ($H > 1$) senescence, we accounted
263 for the phylogenetic relatedness of the species studied to determine the influence of a species'
264 evolutionary history in its likelihood of evolving or escaping senescence. To build the
265 phylogenetic tree with the species included in this study, we used data from the Open Tree of
266 Life³² (OTL), a database that combines public available taxonomic and phylogenetic
267 information across the tree of life. We first checked that the species names in our data were
268 taxonomically accepted using the *taxize* R package³³. Then, we obtained animal and plant
269 phylogenetic trees from OTL for the list of species in our data using *rotl* R package³⁴. The
270 branch length of the resulting tree was computed using the *compute.brlen* function from the R
271 package *ape*³⁵, with Grafen's³⁶ arbitrary branch lengths. Polytomies (*i.e.* > 2 species with the
272 same ancestor) were resolved using the function *multi2di* from *ape* package³⁵, which
273 transforms polytomies into a series of random dichotomies with one or several branches of
274 length zero.

275 To evaluate the role of phylogenetic relatedness in determining the patterns of
276 variation of actuarial senescence we estimated Pagel's λ ¹⁵. This metric is an index bounded

277 between zero and one, where values ~ 0 indicate that the evolutionary history of the species
278 explains little about the variation of the trait measured, and values ~ 1 suggest that that
279 evolutionary history mostly explains the observed variation of the trait across the studied
280 species. To estimate Pagel's λ we used the R package *motmot.2.0*³⁷. A full summary of the
281 phylogenetic signals obtained for each of the four monophyletic groups can be found in the
282 Extended Data and Figures (Table 1).

283 **Reproduction analysis**

284 We calculated reproductive age-trajectories for the species in our analysis to investigate
285 whether reproductive senescence followed the same pattern as actuarial senescence in species
286 that display *vs.* escape actuarial senescence. Age-specific reproduction ($m(x)$) was calculated
287 following Caswell (p. 118-21)¹³. Briefly, the proportional structure of the cohort at age x is
288 given by

$$289 \quad \mathbf{p}(x) = \frac{U^x \mathbf{e}_j}{\mathbf{e}^T U^x \mathbf{e}_j} \quad x = 0, 1, \dots \quad \text{equation 4}$$

290 The total sexual reproductive output per individual at age x is given by

$$291 \quad m(x) = \mathbf{e}^T \mathbf{F} \mathbf{p}(x) \quad \text{equation 5}$$

292

293 For two species, *Araucaria mulleri* and *Juniperus procera*, $m(x)$ was incalculable, and
294 so both species' $l(x)$ and $m(x)$ trajectories are not reported. For the remaining 306 species, the
295 $l(x)$ and $m(x)$ trajectories are found in the Extended Fig. 1a-h.

296

297 **Code availability**

298 Code used for analysis is available in the supplementary information.

299 **Data availability**

300 Data are available from the source data files in the supplementary information and from the

301 COMPADRE Plant Matrix Database and COMADRE Animal Matrix Database

302 (www.compadre-db.com).

303

304 **References**

- 305 1. Medawar, P. B. *An unsolved problem of biology* (H. K. Lewis, 1952).
- 306 2. Salguero-Gómez, R. *et al.* COMADRE: a global database of animal demography. *J.*
307 *Anim. Ecol.* **85**, 371-385 (2016).
- 308 3. Salguero-Gómez, R. *et al.* The COMPADRE plant matrix database: an open online
309 repository for plant demography. *J Ecol.* **103**, 202–218 (2015).
- 310 4. Hamilton, W. D. The moulding of senescence by natural selection. *J. Theor. Biol.* **12**,
311 12–45 (1966).
- 312 5. Williams, G. Pleiotropy, natural selection, and the evolution of senescence. *Evolution*
313 **11**, 398–411 (1957).
- 314 6. Kirkwood, T. B. L. Evolution of ageing. *Nature* **270**, 301–304 (1977).
- 315 7. Jones, O.R., & Vaupel J.W. Senescence is not inevitable. *Biogerontology* **18**, 965-971
316 (2017).
- 317 8. Jones, O.R. *et al.* Diversity of ageing across the tree of life. *Nature* **505**, 169- 174
318 (2014).
- 319 9. Baudisch, A. & Vaupel, J.W. Getting to the root of aging. *Science* **338**, 618–619
320 (2012).
- 321 10. Finch, C. E. *Longevity, Senescence and the Genome* (Univ. Chicago Press, 1994).
- 322 11. Vaupel, J. W., Baudisch, A., Do'lling, M., Roach, D. A. & Gampe, J. The case for
323 negative senescence. *Theor. Popul. Biol.* **65**, 339–351 (2004).
- 324 12. Chiang, C. L. *The life table and its applications* (Krieger Publishing, 1984).
- 325 13. Caswell, H. *Matrix Population Models* (Sinauer Associates, 2001).
- 326 14. Keyfitz, N. *Applied Mathematical Demography* (John Wiley and Sons, 1977).
- 327 15. Pagel, M. Inferring the historical patterns of biological evolution. *Nature.* **401**, 877-
328 884 (1999).

- 329 16. Jones, O.R. *et al.* Senescence rates are determined by ranking on the fast-slow life-
330 history continuum. *Ecology Letters*. **11(7)**, 664-673 (2009).
- 331 17. Lemaître, J-F. & Gaillard, J-M. Reproductive senescence: new perspectives in the
332 wild. *Biol. Rev.* **92(4)**, 2182-2199 (2017).
- 333 18. Barneche, D.R., Robertson, D.R., White, C.R. & Marshall, D.J. Fish reproductive-
334 energy output increases disproportionately with body size. *Science*. **360**, 642-645
335 (2018).
- 336 19. Caswell, H. & Salguero-Gomez, R. Age, stage and senescence in plants. *J.*
337 *Ecol.* **101**, 585–595 (2013).
- 338 20. Baudisch, A. *et al.* The pace and shape of senescence in angiosperms. *J. Ecol.* **101**,
339 596-606 (2013).
- 340 21. Hughes, T. P. Population dynamics based on individual size rather than age: a general
341 model with a reef coral example. *Am. Nat.* **123**, 778-795 (1984).
- 342 22. Caswell, H. Extrinsic mortality and the evolution of senescence. *Trends in Ecology*
343 *and Evolution*. **22**, 173–174 (2007).
- 344 23. Wensink, M.J., Caswell, H. & Baudisch, A. The Rarity of Survival to Old Age Does
345 Not Drive the Evolution of Senescence. *Evol. Biol.* **44**, 5-10 (2017).
- 346 24. Lande, L. A quantitative genetic theory of life history evolution. *Ecology*. **63**, 607–
347 615. (1982).
- 348 25. Bourke, A.F.G. Kin Selection and the Evolutionary Theory of Aging. *Ann. Rev. Ecol.*
349 *Evo. Syst.* **38**, 103-128 (2007).
- 350 26. Hawkes, K., O’Connell, J. F., Blurton-Jones, N. G., Alvarez, H. & Charnov, E. L.
351 Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl*
352 *Acad. Sci. USA*. **95**, 1336–1339 (1998).

- 353 27. Berger, V., Lemaître, J-F., Allainé, D., Gaillard, J-M. & Cohas, A. Early and Adult
354 Social Environments Shape Sex-Specific Actuarial Senescence Patterns in a
355 Cooperative Breeder. *Am. Nat.* **192:4**, 525-536 (2018).
- 356 28. Hammers, M. *et al.* Breeders that receive help age more slowly in a cooperatively
357 breeding bird. *Nature Communications.* **10:1301** (2019).
- 358 29. Jones, O.R. & Salguero- Gómez, R. Life History Trade-Offs Modulate the Speed of
359 Senescence. *The Evolution of Senescence in the Tree of Life*. Eds. Shefferson, R.P.,
360 Jones, O.R. & Salguero-Gómez, R. (Cambridge University Press, 2017).
- 361 30. Salguero-Gómez, R. & Plotkin, JB. Matrix dimensions bias demographic inferences:
362 implications for comparative plant demography. *Am Nat.* **176(6)**, 710-72. (2010).
- 363 31. Horvitz C.C., Tuljapurkar, S. Stage dynamics, period survival, and mortality plateaus.
364 *Am Nat.* **172**, 203–215. (2009).
- 365 32. Hinchliff, C. E. et al. Synthesis of phylogeny and taxonomy into a comprehensive tree
366 of life. *Proc. Natl. Acad. Sci.* **112**, 201423041 (2015).
- 367 33. Chamberlain, S.A. & Szöcs, E. taxize: taxonomic search and retrieval in R.
368 *F1000Research.* (2013).
- 369 34. Michonneau, F., Brown, J. & Winter, D. rotl, an R package to interact with the Open
370 Tree of Life data. *Methods Ecol. Evol.* 1–17. (2016).
- 371 35. Paradis, E., Claude, J. & Strimmer, K. APE: Analyses of phylogenetics and evolution
372 in R language. *Bioinformatics.* **20**, 289–290. (2004).
- 373 36. Grafen, A. The phylogenetic regression. *Phil. Trans. R. Soc. Lond. B.* **326**, 119–157.
374 (1989).
- 375 37. Puttick, M. et al. motmot.2.0: Models of Trait Macroevolution on Trees. R package
376 version 1.1.2. (2018)

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394 **Contributions**

395 M.R. and R.S.G. conceived the project. M.R. and P.C conducted the analysis and produced

396 all visualizations. M.R drafted the first version and together with P.C. and R.S.-G., revised

397 and edited the manuscript.

398 **Competing interests**

399 The authors declare no competing interests.

400 **Corresponding author**

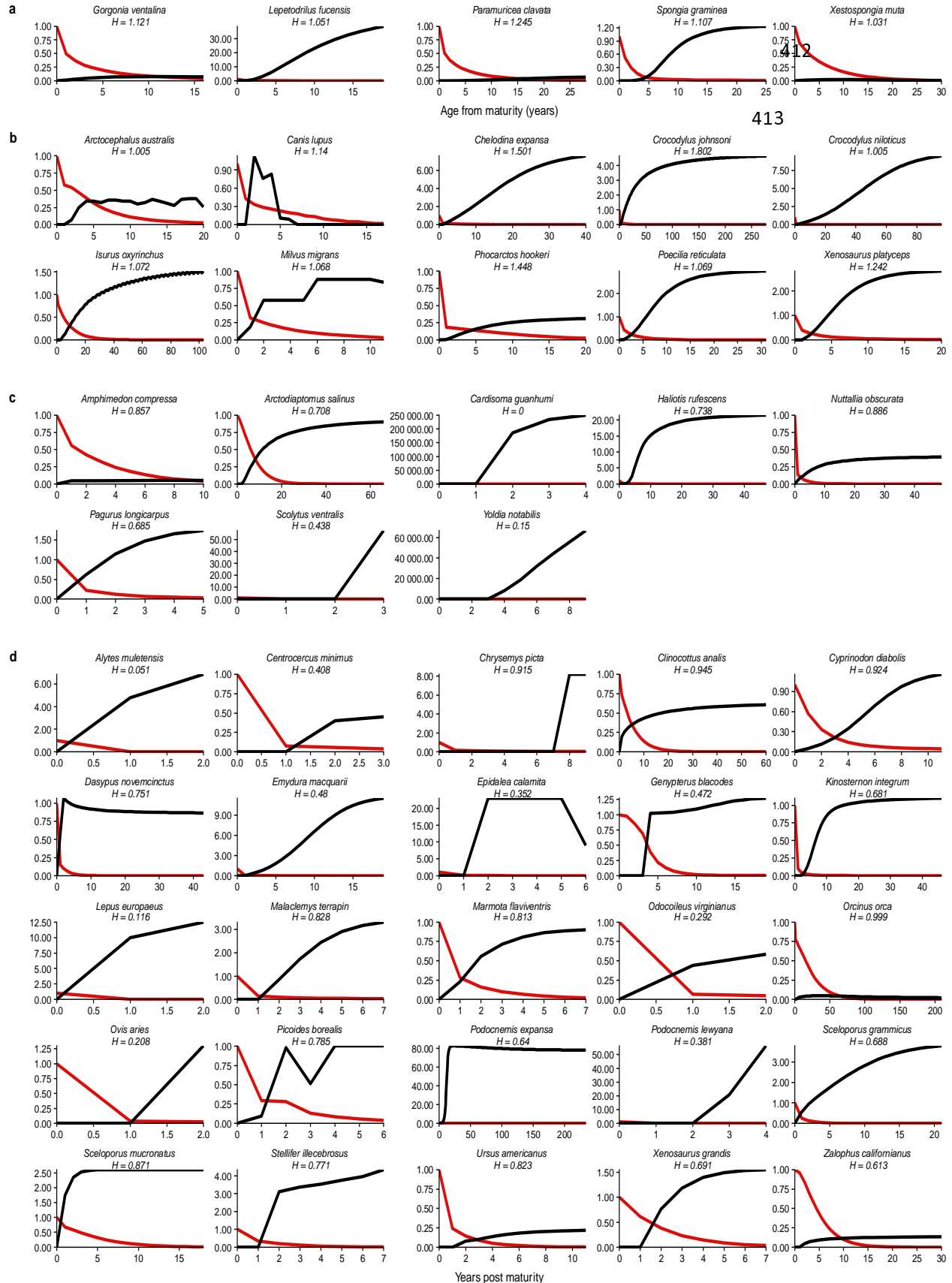
401 Correspondence to Mark Roper, Email mark.roper@keble.ox.ac.uk

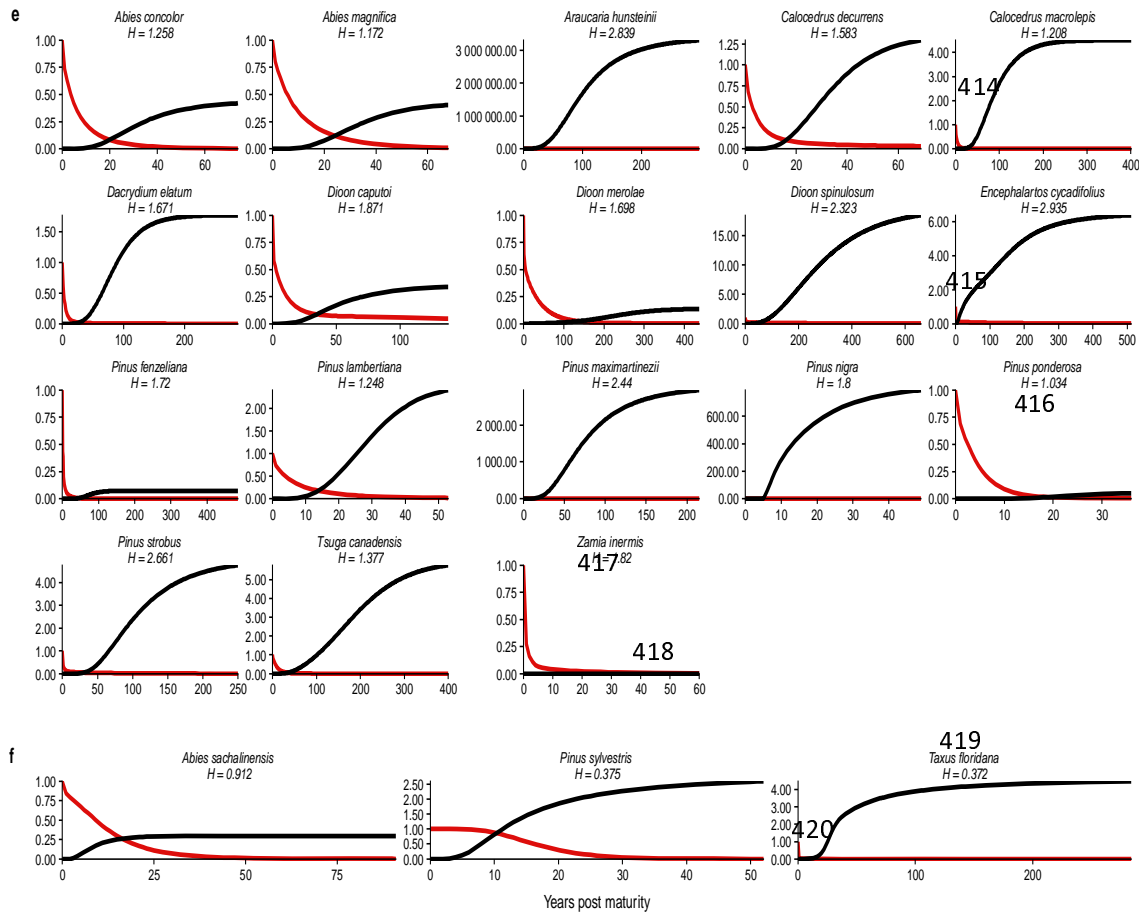
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403 **Extended data figures and tables**

404 **Fig. 1: Survivorship (red) and reproduction (black) age-trajectories for 306 of our study**
405 **species. a)** Invertebrates that escape senescence **b)** Vertebrates that escape senescence **c)**
406 Invertebrates that display senescence **d)** Vertebrates that escape senescence **e)** Gymnosperms
407 that escape senescence **f)** Gymnosperms that display senescence **g)** Angiosperms that escape
408 senescence **h)** Angiosperms that display senescence. Trajectories are conditional upon
409 reaching, and are shown from, the age of maturity, labelled as 0, to the age at which 5% of
410 the mature cohort is still alive. The mature cohort is defined to have survivorship of 1.

411

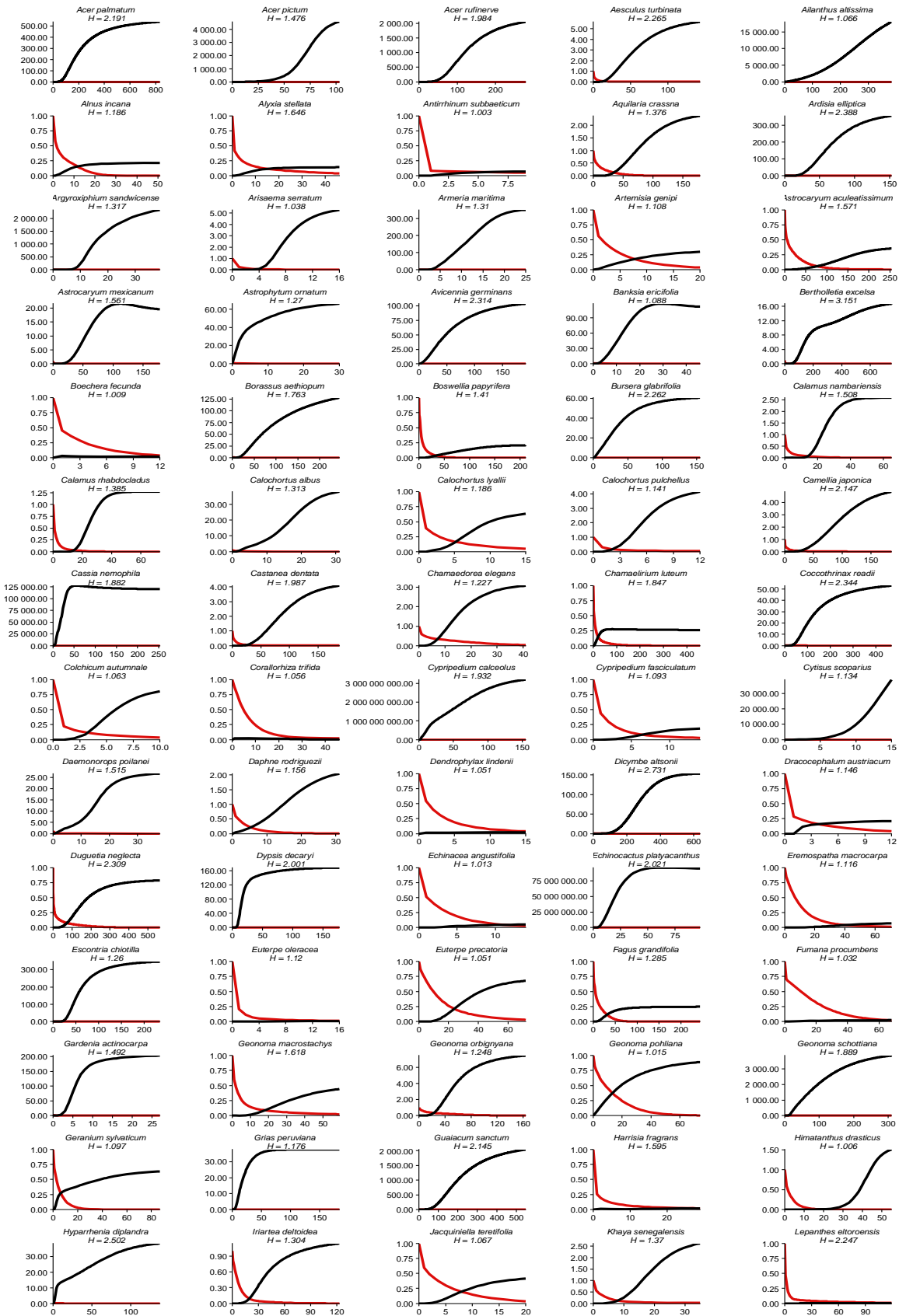


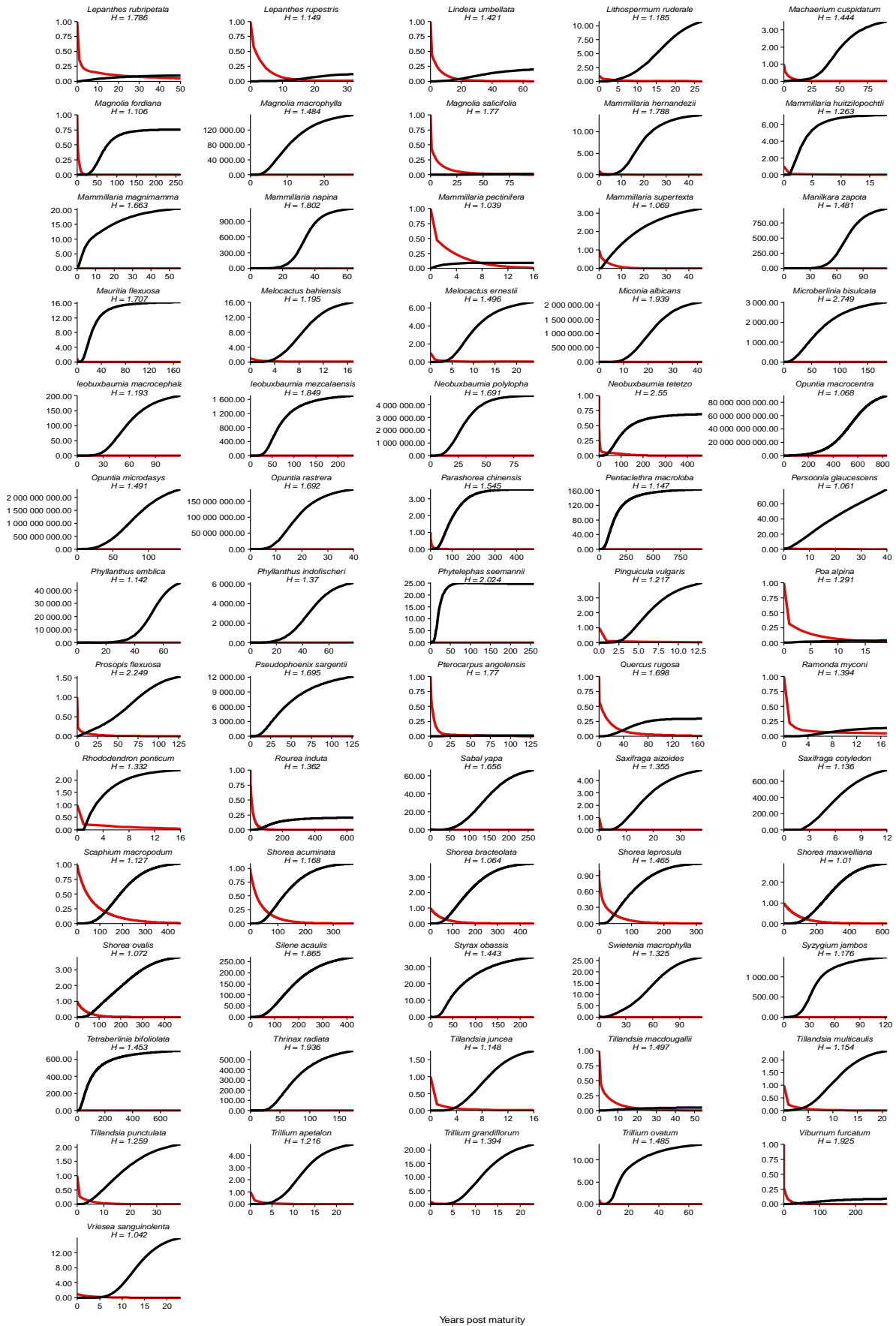


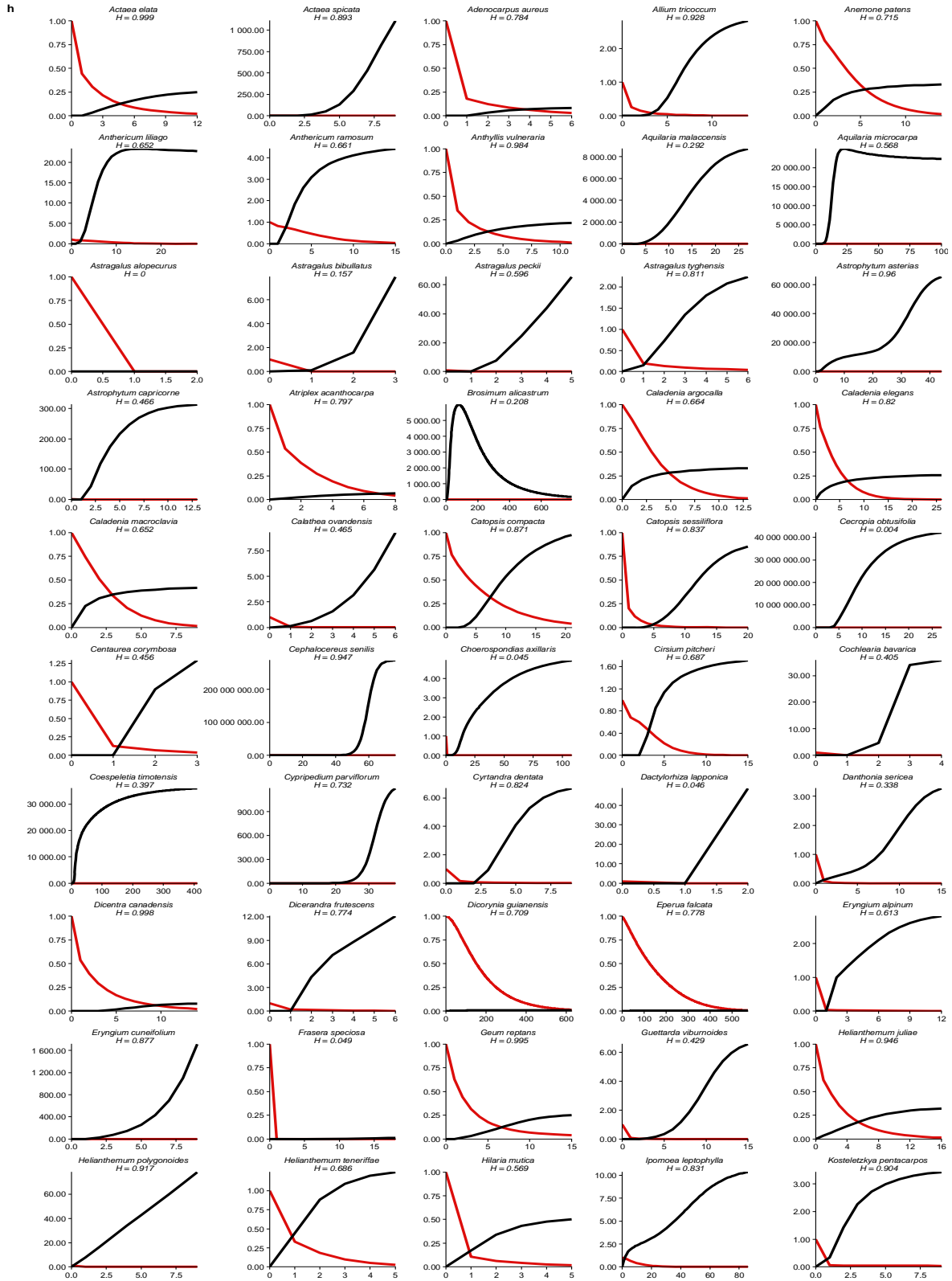
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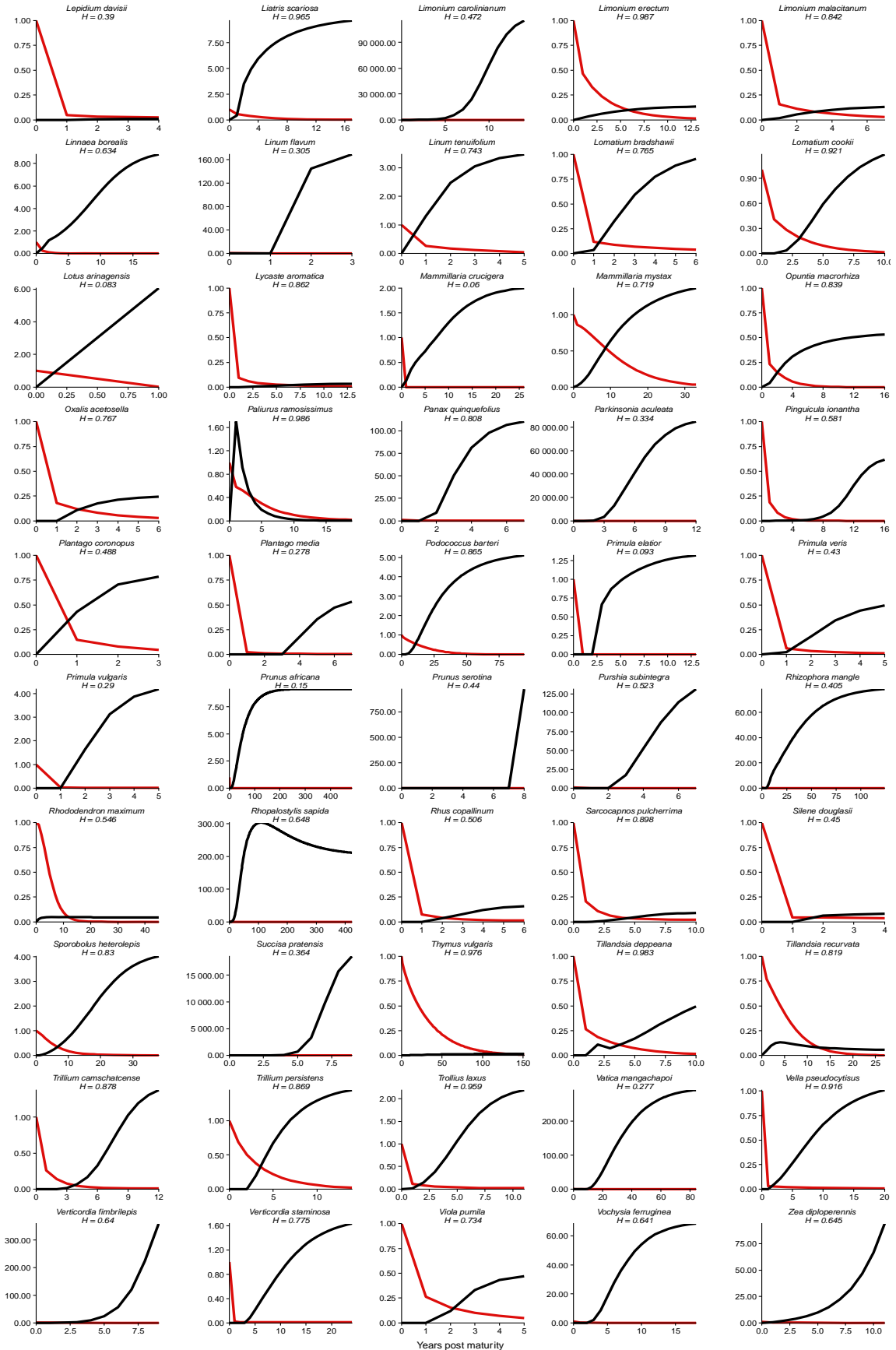






424

425



427 **Extended Data Table 1: Phylogenetic signals of actuarial senescence for each major**
428 **taxonomic group of our 308 studied species are relatively weak.** Calculated estimates of
429 Pagel's λ within the phylogenetic analysis of actuarial senescence across our study species.
430 Pagel's λ is an index bounded between zero and one, where values ~ 0 indicate that the
431 evolutionary history of the species explains little about the variation of the trait measured,
432 and values ~ 1 suggest that that evolutionary history mostly explains the observed variation of
433 the trait across the studied species.
434

Taxonomic breadth	Pagel's λ	5% CI	95% CI
Whole analysis	0.376	0.142	0.654
Plants	0.359	0.077	0.704
Animals	0.000	0.000	0.572
Angiosperms	0.215	0.000	0.687
Gymnosperms	0.000	0.000	0.699
Vertebrates	0.000	0.000	0.658
Invertebrates	0.291	0.000	0.845

435

436 **Supplementary information**

437 **Supplementary Table 1: Study species.** Included species in our analysis were those that
 438 fitted the selection criteria described in methods. Species names, their kingdom (Animalia or
 439 Plantae), whether they display or escape actuarial senescence according to Keyfitz' entropy¹⁴
 440 (H), and the source study from which the data was originally compiled into COMADRE² and
 441 COMPADRE³ are listed.

Species	Kingdom	Actuarial senescence	H	Source
<i>Clinocottus analis</i>	Animalia	Displays senescence	0.945	Davis, J., & Levin, L. Importance of pre-recruitment life-history stages to population dynamics of the woolly sculpin <i>Clinocottus analis</i> . <i>Marine Ecology Progress Series</i> . 234 , 229–246. (2002).
<i>Cyprinodon diabolis</i>	Animalia	Displays senescence	0.924	Beissinger, S. R. Digging the pupfish out of its hole: risk analyses to guide harvest of Devils Hole pupfish for captive breeding. <i>PeerJ</i> . 2 , e549 (2014).
<i>Genypterus blacodes</i>	Animalia	Displays senescence	0.472	González-Olivares, E., Aránguiz-Acuña, A., Ramos-Jiliberto, R., & Rojas-Palma, A. Demographical analysis of the pink ling <i>Genypterus blacodes</i> (Schneider 1801) in the austral demersal fishery: A matrix approach evaluating harvest and non-harvest states. <i>Fisheries Research</i> , 96(2-3) , 216–222. (2009).
<i>Poecilia reticulata</i>	Animalia	Escapes senescence	1.069	Bronikowski, A.M., Clark, M.E., Rodd, F.H. & Reznick, D.N. Population-dynamic consequences of predator-induced life history variation in the guppy (<i>Poecilia reticulata</i>). <i>Ecology</i> . 83(8) , 2194-2204. (2002).
<i>Stellifer illecebrosus</i>	Animalia	Displays senescence	0.771	Foster, S. J., & Vincent, A. C. J. Advice in spite of great uncertainty: assessing and addressing bycatch of small fishes with limited data using <i>Stellifer illecebrosus</i> as a case study. <i>Aquatic Conservation: Marine and Freshwater Ecosystems</i> , 22(5) , 639–651. (2012).
<i>Epidalea calamita</i>	Animalia	Displays senescence		Di Minin, E., & Griffiths, R. A. Viability analysis of a threatened amphibian population: modelling

			0.352	the past, present and future. <i>Ecography</i> , 34(1) , 162–169. (2010).
<i>Gorgonia ventalina</i>	Animalia	Escapes senescence	1.121	Sabat, A.M., & Toledo-Hernandez, C. Viability of Sea Fan Populations Impacted by Disease: Recruitment versus Incidence. <i>Journal of Marine Biology</i> . Vol 2015, Article ID 987060. (2015).
<i>Paramuricea clavata</i>	Animalia	Escapes senescence	1.245	Linares, C., & Doak, D. Forecasting the combined effects of disparate disturbances on the persistence of long-lived gorgonians: a case study of <i>Paramuricea clavata</i> . <i>Marine Ecology Progress Series</i> , 402 , 59–68. (2010).
<i>Centrocercus minimus</i>	Animalia	Displays senescence	0.408	Davis, A. J., Hooten, M. B., Phillips, M. L., & Doherty, P. F. An integrated modeling approach to estimating Gunnison sage-grouse population dynamics: combining index and demographic data. <i>Ecology and Evolution</i> , 4(22) , 4247-4257 (2014).
<i>Milvus migrans</i>	Animalia	Escapes senescence	1.068	Sergio, F., Tavecchia, G., Blas, J., López, L., Tanferna, A., & Hiraldo, F. Variation in age-structured vital rates of a long-lived raptor: Implications for population growth. <i>Basic and Applied Ecology</i> , 12(2) , 107–115. (2011).
<i>Picoides borealis</i>	Animalia	Displays senescence	0.785	Maguire, L. A., Wilhere, G. F., & Dong, Q. Population Viability Analysis for Red-Cockaded Woodpeckers in the Georgia Piedmont. <i>The Journal of Wildlife Management</i> , 59(3) , 533. (1995).
<i>Nuttallia obscurata</i>	Animalia	Displays senescence	0.886	Dudas, S. E., Dower, J. F., & Anholt, B. R. Invasion dynamics of the varnish clam (<i>Nuttallia obscurata</i>): A matrix demographic modelling approach. <i>Ecology</i> , 88(8) , 2084–2093. (2007).
<i>Yoldia notabilis</i>	Animalia	Displays senescence	0.150	Nakaoka, M. Demography of the Marine Bivalve <i>Yoldia notabilis</i> in Fluctuating Environments: An Analysis Using a Stochastic Matrix Model. <i>Oikos</i> , 79(1) , 59.

			(1997).
<i>Amphimedon compressa</i>	Animalia	Displays senescence	0.857 Mercado-Molina, A. E., Sabat, A. M., & Yoshioka, P. M. Demography of the demosponge <i>Amphimedon compressa</i> : Evaluation of the importance of sexual versus asexual recruitment to its population dynamics. <i>Journal of Experimental Marine Biology and Ecology</i> , 407(2) , 355–362. (2011).
<i>Spongia graminea</i>	Animalia	Escapes senescence	1.107 Cropper, W. P., & DiResta, D. Simulation of a Biscayne Bay, Florida commercial sponge population: effects of harvesting after Hurricane Andrew. <i>Ecological Modelling</i> , 118(1) , 1–15. (1999).
<i>Xestospongia muta</i>	Animalia	Escapes senescence	1.031 Pawlik, J., McMurray, S., & Henkel, T. Abiotic factors control sponge ecology in Florida mangroves. <i>Marine Ecology Progress Series</i> , 339 , 93–98. (2007).
<i>Isurus oxyrinchus</i>	Animalia	Escapes senescence	1.072 Tsai, W.-P., Sun, C.-L., Punt, A. E., & Liu, K.-M. Demographic analysis of the shortfin mako shark, <i>Isurus oxyrinchus</i> , in the Northwest Pacific using a two-sex stage-based matrix model. <i>ICES Journal of Marine Science</i> , 71(7) , 1604–1618. (2014).
<i>Haliotis rufescens</i>	Animalia	Displays senescence	0.738 Rogers-Bennett, L., & Leaf, R. T. Elasticity Analyses of Size-Based Red And White Abalone Matrix Models: Management And Conservation. <i>Ecological Applications</i> , 16(1) , 213–224. (2006).
<i>Lepetodrilus fucensis</i>	Animalia	Escapes senescence	1.051 Kelly, N., & Metaxas, A. Understanding population dynamics of a numerically dominant species at hydrothermal vents: a matrix modeling approach. <i>Marine Ecology Progress Series</i> , 403 , 113–128. (2010).
<i>Scolytus ventralis</i>	Animalia	Displays senescence	Berryman, A. A. (1973). Population dynamics of the fir engraver, <i>Scolytus ventralis</i> (Coleoptera: Scolytidae). I. Analysis of population behaviour and survival from 1964 to

			0.438	1971. <i>The Canadian Entomologist</i> , 105(11) , 1465–1488. (1973)
<i>Cardisoma guanhumii</i>	Animalia	Displays senescence	0.000	Rodriguez-Fourquet, PhD thesis, 2004.
<i>Pagurus longicarpus</i>	Animalia	Displays senescence	0.685	Damiani, C. C. (2005). Integrating direct effects and trait-mediated indirect effects using a projection matrix model. <i>Ecology</i> , 86(8) , 2068–2074. (2005).
<i>Canis lupus familiaris</i>	Animalia	Escapes senescence	1.140	Makenov, M. T., & Bekova, S. K. Demography of domestic dog population and its implications for stray dog abundance: a case study of Omsk, Russia. <i>Urban Ecosystems</i> , 19(3) , 1405–1418. (2016).
<i>Lepus europaeus</i>	Animalia	Displays senescence	0.116	Marboutin, E., & Peroux, R. Survival Pattern of European Hare in a Decreasing Population. <i>The Journal of Applied Ecology</i> , 32(4) , 809. (1995).
<i>Marmota flaviventris</i>	Animalia	Displays senescence	0.813	Ozgul, A., Oli, M. K., Armitage, K. B., Blumstein, D. T., & Van Vuren, D. H. Influence of Local Demography on Asymptotic and Transient Dynamics of a Yellow-Bellied Marmot Metapopulation. <i>Am. Nat.</i> 173(4) , 517–530. (2009).
<i>Odocoileus virginianus</i>	Animalia	Displays senescence	0.292	Chitwood, M. C., Lashley, M. A., Kilgo, J. C., Moorman, C. E., & Deperno, C. S. White-tailed deer population dynamics and adult female survival in the presence of a novel predator. <i>The Journal of Wildlife Management</i> , 79(2) , 211–219. (2015).
<i>Orcinus orca</i>	Animalia	Displays senescence	0.998	Velez-Espino, L.A. et al. Comparative demography and viability of northeastern Pacific resident killer whale populations at risk. <i>Can Tech Report Fish & Aq Sci.</i> (2014).
<i>Ovis aries</i>	Animalia	Displays senescence	0.208	Clutton-Brock, T. H., Price, O. F., Albon, S. D., & Jewell, P. A. Early Development and Population Fluctuations in Soay Sheep. <i>The Journal of Animal Ecology</i> , 61(2) , 381. (1992).
<i>Phocarcotus hookeri</i>	Animalia	Escapes senescence		Meyer, S., Robertson, B. C., Chilvers, B. L., & Krkošek, M. Population dynamics reveal conservation priorities of the threatened New Zealand sea lion

			1.448	<i>Phocarcos hookeri</i> . <i>Marine Biology</i> , 162(8) , 1587–1596. (2015).
<i>Ursus americanus</i>	Animalia	Displays senescence	0.823	Lewis, D. L., Breck, S. W., Wilson, K. R., & Webb, C. T. Modeling black bear population dynamics in a human-dominated stochastic environment. <i>Ecological Modelling</i> , 294 , 51–58. (2014).
<i>Zalophus californianus</i>	Animalia	Displays senescence	0.612	Wielgus, J., Gonzalez-Suarez, M., Auriol-Gamboa, D., & Gerber, L. R. A noninvasive demographic assessment of sea lions base don stage-specific abundances. <i>Ecological Applications</i> , 18(5) , 1287–1296. (2008).
<i>Arctodiaptomus salinus</i>	Animalia	Displays senescence	0.708	Jiménez-Melero, R., Gilbert, J., & Guerrero, F. Secondary production of <i>Arctodiaptomus salinus</i> in a shallow saline pond: comparison of methods. <i>Marine Ecology Progress Series</i> , 483 , 103–116. (2013).
<i>Chelodina expansa</i>	Animalia	Escapes senescence	1.501	Spencer, R.J., & Thompson, M.B. Experimental Analysis of the Impact of Foxes on Freshwater Turtle Populations. <i>Conservation Biology</i> , 19(3) , 845–854. (2005).
<i>Chrysemys picta</i>	Animalia	Displays senescence	0.915	Mitchell, J. C. Population Ecology and Life Histories of the Freshwater Turtles <i>Chrysemys picta</i> and <i>Sternotherus odoratus</i> in an Urban Lake. <i>Herpetological Monographs</i> , 2 , 40. (1988).
<i>Crocodylus johnsoni</i>	Animalia	Escapes senescence	1.802	Tucker, PhD Thesis, 1997. Smith, A.M.A & Webb, G.J.W. <i>Crocodylus johnsoni</i> in the McKinlay Area, N.T. VIII. A Population Simulation Model: <i>Wildlife Research</i> 12 , 541-554. (1985)
<i>Crocodylus niloticus</i>	Animalia	Escapes senescence	1.005	Hutton, PhD thesis, 1984.
<i>Emydura macquarii</i>	Animalia	Displays senescence	0.480	SPENCER, R.-J., & THOMPSON, M. B. (2005). Experimental Analysis of the Impact of Foxes on Freshwater Turtle Populations. <i>Conservation Biology</i> , 19(3) , 845–854. (2005).
<i>Kinosternon</i>	Animalia	Displays senescence		Macip-Rios, R. et al.

<i>integrum</i>			0.681	Demography of two populations of the Mexican mud turtle (<i>Kinosternon integrum</i>) in central Mexico. <i>Herp J.</i> 21(4) , 235-245. (2011).
<i>Malaclemys terrapin</i>	Animalia	Displays senescence	0.828	Crawford, B. A., Maerz, J. C., Nibbelink, N. P., Buhlmann, K. A., & Norton, T. M. Estimating the consequences of multiple threats and management strategies for semi-aquatic turtles. <i>Journal of Applied Ecology</i> , <i>51(2)</i> , 359–366. (2014).
<i>Podocnemis lewyana</i>	Animalia	Displays senescence	0.381	Páez, V. P., Bock, B. C., Espinal-García, P. A., Rendón-Valencia, B. H., Alzate-Estrada, D., Cartagena-Otálvaro, V. M., & Heppell, S. S. Life History and Demographic Characteristics of the Magdalena River Turtle (<i>Podocnemis lewyana</i>): Implications for Management. <i>Copeia</i> , 103(4) , 1058–1074. (2015).
<i>Podocnemis expansa</i>	Animalia	Displays senescence	0.640	Mogollones, S. C., Rodríguez, D. J., Hernández, O., & Barreto, G. R. A Demographic Study of the Arrau Turtle (<i>Podocnemis expansa</i>) in the Middle Orinoco River, Venezuela. <i>Chelonian Conservation and Biology</i> , 9(1) , 79–89. (2010).
<i>Sceloporus grammicus</i>	Animalia	Displays senescence	0.688	Pérez-Mendoza, H. A., Zúñiga-Vega, J. J., Zurita-Gutiérrez, Y. H., Fornoni, J., Solano-Zavaleta, I., Hernández-Rosas, A. L., & Molina-Moctezuma, A. Demographic Importance of the Life-Cycle Components in <i>Sceloporus grammicus</i> . <i>Herpetologica</i> , 69(4) , 411–435. (2013).
<i>Sceloporus mucronatus</i>	Animalia	Displays senescence	0.871	Ortega-Leon, A.M., Smith, E.R., Zúñiga-Vega, J. J & Mendez-de la Cruz, F.R. Growth and demography of one population of the lizard <i>Sceloporus mucronatus</i> . <i>West N Am Naturalist</i> . 67(4) , 492-502. (2007).
<i>Xenosaurus grandis</i>	Animalia	Displays senescence		Zúñiga-Vega, J. J., Valverde, T., Rojas-Gonzalez, R.I. & Lemos-Espinal, J.A. Analysis of the population dynamics of an

			0.691	endangered lizard (<i>Xenosaurus grandis</i>) through the use of projection matrices. <i>Copeia</i> . 2, 324-335. (2007).
<i>Xenosaurus platyceps</i>	Animalia	Escapes senescence	1.242	Jones, C., Rojas-González, I., Lemos-Espinal, J., & Zúñiga-Vega, J. Demography of <i>Xenosaurus platyceps</i> (Squamata: Xenosauridae): a comparison between tropical and temperate populations. <i>Amphibia-Reptilia</i> , 29(2) , 245–256. (2008).
			0.051	Pinya, S., Tavecchia, G. & Perez-Mellado, V. Population model of an endangered amphibian: implications for conservation management. <i>Endangered Species Research</i> . 34 , 123-130. (2017).
<i>Alytes muletensis</i>	Animalia	Displays senescence	1.004	Lima, M. & Paez, E. Demography and Population Dynamics of South American Fur Seals. <i>Journal of Mammalogy</i> . 78(3) , 914-920. (1997).
<i>Arctocephalus australis</i>	Animalia	Escapes senescence	0.751	Oli, M.K. <i>et al.</i> Dynamics of leprosy in nine-banded armadillos: Net reproductive number and effects on host population dynamics. <i>Ecological Modelling</i> . 350 , 100-108. (2017).
<i>Dasybus novemcinctus</i>	Animalia	Displays senescence		Zotz, G., & Schmidt, G. Population decline in the epiphytic orchid <i>Aspasia principissa</i> . <i>Biological Conservation</i> , 129(1) , 82–90. (2006).
<i>Aspasia principissa</i>	Plantae	Escapes senescence	1.163	
			0.871	Del Castillo, R. F., Trujillo-Argueta, S., Rivera-García, R., Gómez-Ocampo, Z., & Mondragón-Chaparro, D. Possible combined effects of climate change, deforestation, and harvesting on the epiphyte <i>Catopsis compacta</i> : a multidisciplinary approach. <i>Ecology and Evolution</i> , 3(11) , 3935–3946. (2013).
<i>Catopsis compacta</i>	Plantae	Displays senescence		
			0.837	Winkler, M., Hülber, K., & Hietz, P. Population dynamics of epiphytic bromeliads: Life strategies and the role of host branches. <i>Basic and Applied Ecology</i> , 8(2) , 183–196. (2007).
<i>Catopsis sessiliflora</i>	Plantae	Displays senescence		
<i>Jacquinilla teretifolia</i>	Plantae	Escapes senescence		Winkler, M., Hülber, K., & Hietz, P. Population dynamics of

			1.067	epiphytic orchids in a metapopulation context. <i>Annals of Botany</i> , 104(5) , 995–1004. (2009).
<i>Lepanthes eltoroensis</i>	Plantae	Escapes senescence	2.247	Tremblay, R.L. & Ackerman, J.D. Gene flow and effective population size in <i>Lepanthes</i> (<i>Orchidaceae</i>): a case for genetic drift. <i>Biological Journal of the Linnean Society</i> , 72(1) , 47–62. (2001).
<i>Lepanthes rubripetala</i>	Plantae	Escapes senescence	1.786	Schödelbauerová I., Tremblay, R. L., & Kindlmann, P. Prediction vs. reality: Can a PVA model predict population persistence 13 years later? <i>Biodiversity and Conservation</i> . 19(3) , 637-650. (2009).
<i>Lycaste aromatica</i>	Plantae	Displays senescence	0.862	Winkler, M., Hülber, K., & Hietz, P. Population dynamics of epiphytic orchids in a metapopulation context. <i>Annals of Botany</i> , 104(5) , 995–1004. (2009).
<i>Tillandsia depeana</i>	Plantae	Displays senescence	0.983	Winkler, M., Hülber, K., & Hietz, P. Population dynamics of epiphytic bromeliads: Life strategies and the role of host branches. <i>Basic and Applied Ecology</i> , 8(2) , 183–196. (2007).
<i>Tillandsia juncea</i>	Plantae	Escapes senescence	1.142	Winkler, M., Hülber, K., & Hietz, P. Population dynamics of epiphytic bromeliads: Life strategies and the role of host branches. <i>Basic and Applied Ecology</i> , 8(2) , 183–196. (2007).
<i>Tillandsia macdougallii</i>	Plantae	Escapes senescence	1.500	Mondragon Chopparo D., & Ticktin, T. Demographic Effects of Harvesting Epiphytic Bromeliads and an Alternative Approach to Collection. <i>Conservation Biology</i> , 25(4) , 797–807. (2011).
<i>Tillandsia multicaulis</i>	Plantae	Escapes senescence	1.154	Winkler, M., Hülber, K., & Hietz, P. Population dynamics of epiphytic bromeliads: Life strategies and the role of host branches. <i>Basic and Applied Ecology</i> , 8(2) , 183–196. (2007).
<i>Tillandsia punctulata</i>	Plantae	Escapes senescence		Toledo-Aceves, T., Hernández-Apolinar, M., & Valverde, T. Potential impact of harvesting on

			1.259	the population dynamics of two epiphytic bromeliads. <i>Acta Oecologica</i> , 59 , 52–61. (2014).
<i>Tillandsia recurvata</i>	Plantae	Displays senescence	0.819	Valverde, T. & Rocio, B. Is there demographic asynchrony among local populations of <i>Tillandsia recurvata</i> ? Evidence of its metapopulation functioning. <i>Bol. Soc. Bot. Mex.</i> n.86 (2010).
<i>Vriesea sanguinolenta</i>	Plantae	Escapes senescence	1.042	Zotz, G. Differences in vital demographic rates in three populations of the epiphytic bromeliad, <i>Werauhia sanguinolenta</i> . <i>Acta Oecologica</i> , 28(3) , 306–312. (2005).
<i>Actaea spicata</i>	Plantae	Displays senescence	0.893	Fröborg, H., & Eriksson, O. Predispersal seed predation and population dynamics in the perennial understorey herb <i>Actaea spicata</i> . <i>Canadian Journal of Botany</i> , 81(11) , 1058–1069. (2003).
<i>Adenocarpus aureus gibbsianus</i>	Plantae	Displays senescence	0.784	Iriondo; Albert; Giménez; Lozano; Escudero (2009). Book.
<i>Allium tricoccum</i>	Plantae	Displays senescence	0.928	Nault, A., & Gagnon, D. Ramet Demography of <i>Allium tricoccum</i> , A Spring Ephemeral, Perennial Forest Herb. <i>The Journal of Ecology</i> , 81(1) , 101. (1993).
<i>Anemone patens</i>	Plantae	Displays senescence	0.715	Williams, J.L. & Crone, E.E. The impact of invasive grasses on the population growth of <i>Anemone patens</i> , a long-lived native forb. <i>Ecology</i> . 87 (12) 3200-3208 (2006).
<i>Anthericum liliago</i>	Plantae	Displays senescence	0.652	Cerná, L., & Münzbergová, Z. (2013). Comparative Population Dynamics of Two Closely Related Species Differing in Ploidy Level. <i>PLoS ONE</i> . 8(10) , e75563. (2013).
<i>Anthericum ramosum</i>	Plantae	Displays senescence	0.661	Cerná, L., & Münzbergová, Z. Comparative Population Dynamics of Two Closely Related Species Differing in Ploidy Level. <i>PLoS ONE</i> . 8(10) , e75563. (2013).
<i>Anthyllis vulneraria alpicola</i>	Plantae	Displays senescence		Marcante, S., Winkler, E., & Erschbamer, B. Population dynamics along a primary

			0.984	succession gradient: do alpine species fit into demographic succession theory? <i>Annals of Botany</i> . 103(7) , 1129–1143. (2009).
<i>Antirrhinum subbaeticum</i>	Plantae	Escapes senescence	1.003	Iriondo; Albert; Gimenez; Lozana; Escuerdo. 978-84-8014-746-0
<i>Boechera fecunda</i>	Plantae	Escapes senescence	1.009	Lesica, P., & Shelly, J. S. Effects of reproductive mode on demography and life history in <i>Arabis fecunda</i> (Brassicaceae). <i>American Journal of Botany</i> . 82(6) , 752–762. (1995).
<i>Arisaema serratum</i>	Plantae	Escapes senescence	1.034	Kinoshita, E. Sex Change and Population Dynamics in <i>Arisaema serratum</i> . <i>Plant Species Biology</i> . 2(1-2) , 15–28. (1987).
<i>Armeria maritima</i>	Plantae	Escapes senescence	1.310	Lefebvre, C., & Chandler-Mortimer, A. Demographic Characteristics of the Perennial Herb <i>Armeria maritima</i> on Zilc Lead Mine Wastes. <i>The Journal of Applied Ecology</i> . 21(1) , 255. (1984).
<i>Artemisia genipi</i>	Plantae	Escapes senescence	1.108	Marcante, S., Winkler, E., & Erschbamer, B. Population dynamics along a primary succession gradient: do alpine species fit into demographic succession theory? <i>Annals of Botany</i> . 103(7) , 1129–1143. (2009).
<i>Astragalus alopecurus</i>	Plantae	Displays senescence	0.000	Nicole, PhD thesis, 2005
<i>Astragalus peckii</i>	Plantae	Displays senescence	0.596	Martin, E. F., & Meinke, R. J. Variation in the demographics of a rare central Oregon endemic, <i>Astragalus peckii</i> Piper (Fabaceae), with fluctuating levels of herbivory. <i>Population Ecology</i> . 54(3) , 381–390. (2012).
<i>Astragalus tyghensis</i>	Plantae	Displays senescence	0.811	Kaye, T.N. & Pyke, D.A. The effect of stochastic technique on estimates of population viability from transition matrix models. <i>Ecology</i> . 84(6) , 1464-1476. (2003).
<i>Calathea ovandensis</i>	Plantae	Displays senescence		Horvitz, C. C., & Schemske, D. W. Spatiotemporal Variation in Demographic Transitions of a Tropical Understory Herb: Projection Matrix Analysis.

			0.465	<i>Ecological Monographs</i> . 65(2) , 155–192. (1995).
<i>Calochortus albus</i>	Plantae	Escapes senescence	1.313	Fiedler, P. L. Life History and Population Dynamics of Rare and Common Mariposa Lilies (<i>Calochortus Pursh</i> : Liliaceae). <i>The Journal of Ecology</i> . 75(4) , 977. (1987).
<i>Calochortus lyallii</i>	Plantae	Escapes senescence	1.186	Allen, PhD thesis, 2004.
<i>Calochortus pulchellus</i>	Plantae	Escapes senescence	1.141	Fiedler, P. L. Life History and Population Dynamics of Rare and Common Mariposa Lilies (<i>Calochortus Pursh</i> : Liliaceae). <i>The Journal of Ecology</i> . 75(4) , 977. (1987).
<i>Chamaelirium luteum</i>	Plantae	Escapes senescence	1.185	Meagher, T. R., & Antonovics, J. The Population Biology of <i>Chamaelirium Luteum</i> , A Dioecious Member of the Lily Family: Life History Studies. <i>Ecology</i> . 63(6) , 1690. (1982).
<i>Actaea elata</i>	Plantae	Displays senescence	0.999	Kaye, T.N. & Pyke, D.A. The effect of stochastic technique on estimates of population viability from transition matrix models. <i>Ecology</i> . 84(6) 1464-1476. (2003).
<i>Cochlearia bavarica</i>	Plantae	Displays senescence	0.405	Abs, C. Differences in the life histories of two Cochlearia species. <i>Folia Geobotanica</i> , 34(1) , 33–45. (1999).
<i>Colchicum autumnale</i>	Plantae	Escapes senescence	1.063	Winter, S., Jung, L. S., Eckstein, R. L., Otte, A., Donath, T. W., & Kriechbaum, M. Control of the toxic plant <i>Colchicum autumnale</i> in semi-natural grasslands: effects of cutting treatments on demography and diversity. <i>Journal of Applied Ecology</i> . 51(2) , 524–533. (2014).
<i>Corallorhiza trifida</i>	Plantae	Escapes senescence	1.056	Iriondo; Albert; Gimenez; Lozana; Escuerdo 978-84-8014-746-0
<i>Cypripedium calceolus</i>	Plantae	Escapes senescence	1.932	Nicole, F., Brzosko, E., & Till-Bottraud, I. Population viability analysis of <i>Cypripedium calceolus</i> in a protected area: longevity, stability and persistence. <i>Journal of Ecology</i> . 93(4) , 716–726. (2005).
<i>Cypripedium fasciculatum</i>	Plantae	Escapes senescence		Crone, E.E. <i>et al.</i> Ability of Matrix Models to Explain the Past and Predict the Future of Plant

			1.093	Populations. <i>Conservation Biology</i> . 27(5) , 968-978. (2013).
<i>Cypripedium parviflorum</i>	Plantae	Displays senescence	0.732	Shefferson, R.P., Warren, R.J. & Pulliam, H.R. Life-history costs make perfect sprouting maladaptive in two herbaceous perennials. <i>Journal of Ecology</i> . 102(5) , 1318-1328. (2014).
<i>Dactylorhiza lapponica</i>	Plantae	Displays senescence	10.46	Sletvold, N., Øien, D.-I., & Moen, A. Long-term influence of mowing on population dynamics in the rare orchid <i>Dactylorhiza lapponica</i> : The importance of recruitment and seed production. <i>Biological Conservation</i> . 143(3) , 747-755. (2010).
<i>Danthonia sericea</i>	Plantae	Displays senescence	0.338	Moloney, K. A. Fine-Scale Spatial and Temporal Variation in the Demography of a Perennial Bunchgrass. <i>Ecology</i> . 69(5) , 1588-1598. (1988).
<i>Dicentra canadensis</i>	Plantae	Displays senescence	0.998	Lin, C.-H., Miriti, M. N., & Goodell, K. (Demographic consequences of greater clonal than sexual reproduction in <i>Dicentra canadensis</i> . <i>Ecology and Evolution</i> . 6(12) , 3871-3883. (2016).
<i>Dicerandra frutescens</i>	Plantae	Displays senescence	0.774	Menges, E. S., Quintana Ascencio, P. F., Weekley, C. W., & Gaoue, O. G. Population viability analysis and fire return intervals for an endemic Florida scrub mint. <i>Biological Conservation</i> . 127(1) , 115-127. (2006).
<i>Dracocephalum austriacum</i>	Plantae	Escapes senescence	1.146	Andrello, PhD thesis, 2010.
<i>Eryngium alpinum</i>	Plantae	Escapes senescence	0.613	Andrello, M. <i>et al.</i> Effects of management regimes and extreme climatic events on plant population viability in <i>Eryngium alpinum</i> . <i>Biological Conservation</i> . 147(1) , 99-106. (2012).
<i>Eryngium cuneifolium</i>	Plantae	Displays senescence	0.877	Menges, E. S., & Quintana-Ascencio, P. F. Population viability with fire in <i>Eryngium cuneifolium</i> : deciphering a decade of demographic data. <i>Ecological Monographs</i> . 74(1) , 79-99. (2004).
<i>Geranium sylvaticum</i>	Plantae	Escapes senescence		Ramula, S., Toivonen, E., & Mutikainen, P. Demographic

			1.097	Consequences of Pollen Limitation and Inbreeding Depression in a Gynodioecious Herb. <i>International Journal of Plant Sciences</i> . 168(4) , 443–453. (2007).
<i>Geum reptans</i>	Plantae	Displays senescence	0.995	Weppler, T., Stoll, P., & Stocklin, J. The relative importance of sexual and clonal reproduction for population growth in the long-lived alpine plant <i>Geum reptans</i> . <i>Journal of Ecology</i> . 94(4) , 869–879. (2006).
<i>Helianthemum polygonoides</i>	Plantae	Displays senescence	0.917	Iriondo; Albert; Gimenez; Lozana; Escuerdo 978-84-8014-746-0
<i>Helianthemum teneriffae</i>	Plantae	Displays senescence	0.686	Iriondo; Albert; Gimenez; Lozana; Escuerdo 978-84-8014-746-0
<i>Hilaria mutica</i>	Plantae	Displays senescence	0.569	Vega, E., & Montaña, C. Spatio-temporal variation in the demography of a bunch grass in a patchy semiarid environment. <i>Plant Ecology Formerly 'Vegetatio'</i> . 175(1) , 107–120. (2004).
<i>Hyparrhenia diplandra</i>	Plantae	Escapes senescence	2.502	Garnier, L.K.M. & Dajoz, I. Evolutionary significance of awn length variation in a clonal grass of fire-prone savannas. <i>Ecology</i> . 82(6) , 1720-1733. (2001).
<i>Ipomoea leptophylla</i>	Plantae	Displays senescence	0.831	Keeler, K. H. Survivorship and Recruitment in a Long-lived Prairie Perennial, <i>Ipomoea leptophylla</i> (Convolvulaceae). <i>American Midland Naturalist</i> . 126(1) , 44. (1991).
<i>Kosteletzkya pentacarpos</i>	Plantae	Displays senescence	0.904	Pino, J., Pico, F. X., & De Roa, E. Population dynamics of the rare plant <i>Kosteletzkya pentacarpos</i> (Malvaceae): a nine-year study. <i>Botanical Journal of the Linnean Society</i> . 153(4) , 455–462. (2007).
<i>Lepanthes rupestris</i>	Plantae	Escapes senescence	1.145	Tremblay, R. L., & Ackerman J. D. Gene flow and effective population size in <i>Lepanthes</i> (Orchidaceae): a case for genetic drift. <i>Biological Journal of the Linnean Society</i> . 72(1) , 47–62. (2001).
<i>Lepidium davisii</i>	Plantae	Displays senescence	0.390	Bernatus, Report, 1995.
<i>Liatrix scariosa</i>	Plantae	Displays senescence		Ellis, M. M. <i>et al.</i> Matrix population models from 20

			0.965	studies of perennial plant populations. <i>Ecology</i> . 93(4) , 951–951. (2012).
<i>Limonium carolinianum</i>	Plantae	Displays senescence	0.472	Baltzer, J. L., Reekie, E. G., Hewlin, H. L., Taylor, P. D., & Boates, J. S. Impact of flower harvesting on the salt marsh plant <i>Limonium carolinianum</i> . <i>Canadian Journal of Botany</i> . 80(8) , 841–851. (2002).
<i>Limonium erectum</i>	Plantae	Displays senescence	0.987	Iriondo; Albert; Gimenez; Lozana; Escuerdo 978-84-8014-746-0
<i>Limonium malacitanum</i>	Plantae	Displays senescence	0.842	Iriondo; Albert; Gimenez; Lozana; Escuerdo 978-84-8014-746-0
<i>Linum flavum</i>	Plantae	Displays senescence	0.305	Münzbergová, Z. Comparative demography of two co-occurring <i>Linum</i> species with different distribution patterns. <i>Plant Biology</i> . 15(6) , 963–970. (2013).
<i>Linum tenuifolium</i>	Plantae	Displays senescence	0.743	Münzbergová, Z. Comparative demography of two co-occurring <i>Linum</i> species with different distribution patterns. <i>Plant Biology</i> . 15(6) , 963–970. (2013).
<i>Lithospermum ruderale</i>	Plantae	Escapes senescence	1.185	Bricker, M., & Maron, J. Post dispersal seed predation limits the abundance of a long-lived perennial forb (<i>Lithospermum ruderale</i>). <i>Ecology</i> . 93(3) , 532–543. (2012).
<i>Lomatium bradshawii</i>	Plantae	Displays senescence	0.765	Kaye, T.N. & Pyke, D.A. The effect of stochastic technique on estimates of population viability from transition matrix models. <i>Ecology</i> . 84(6) , 1464-1476 (2003).
<i>Lomatium cookii</i>	Plantae	Displays senescence	0.921	Kaye, T.N. & Pyke, D.A. The effect of stochastic technique on estimates of population viability from transition matrix models. <i>Ecology</i> . 84(6) , 1464-1476 (2003).
<i>Lotus arinagensis</i>	Plantae	Displays senescence	0.083	Iriondo; Albert; Gimenez; Lozana; Escuerdo 978-84-8014-746-0
<i>Oxalis acetosella</i>	Plantae	Displays senescence	0.767	Berg, H. Population dynamics in <i>Oxalis acetosella</i> : the significance of sexual reproduction in a clonal, cleistogamous forest herb. <i>Ecography</i> . 25(2) , 233–243. (2002).
<i>Panax</i>	Plantae	Displays senescence		Charron, D., & Gagnon, D. The

<i>quinquefolius</i>			0.801	Demography of Northern Populations of <i>Panax Quinquefolium</i> (American Ginseng). <i>The Journal of Ecology</i> . 79(2) , 431. (1991).
<i>Pinguicula ionantha</i>	Plantae	Displays senescence	0.581	Kesler, H. C., Trusty, J. L., Hermann, S. M., & Guyer, C. Demographic responses of <i>Pinguicula ionantha</i> to prescribed fire: a regression-design LTRE approach. <i>Oecologia</i> . 156(3) , 545–557. (2008).
<i>Pinguicula vulgaris</i>	Plantae	Escapes senescence	1.217	Svensson, B. M., Carlsson, B. A., Karlsson, P. S., & Nordell, K. O. Comparative Long-Term Demography of Three Species of <i>Pinguicula</i> . <i>The Journal of Ecology</i> . 81(4) , 635. (1993).
<i>Plantago coronopus</i>	Plantae	Displays senescence	0.488	Villellas, J. <i>et al.</i> Plant performance in central and northern peripheral populations of the widespread <i>Plantago coronopus</i> . <i>Ecography</i> . 36(2) , 136-145. (2012).
<i>Plantago media</i>	Plantae	Displays senescence	0.273	Eriksson, Å., & Eriksson, O. Population dynamics of the perennial <i>Plantago media</i> in semi-natural grasslands. <i>Journal of Vegetation Science</i> . 11(2) , 245–252. (2000).
<i>Poa alpina</i>	Plantae	Escapes senescence	1.291	Marcante, S., Winkler, E., & Erschbamer, B. Population dynamics along a primary succession gradient: do alpine species fit into demographic succession theory? <i>Annals of Botany</i> . 103(7) , 1129–1143. (2009).
<i>Primula elatior</i>	Plantae	Displays senescence	0.093	Jacquemyn, H., & Brys, R. Effects of stand age on the demography of a temperate forest herb in post-agricultural forests. <i>Ecology</i> . 89(12) , 3480–3489. (2008).
<i>Primula veris</i>	Plantae	Escapes senescence	0.430	Lethilia, K., Syrjanen, K., Leimu, R., Garcia, M. B., & Ehrlén, J. Habitat Change and Demography of <i>Primula veris</i> : Identification of Management Targets. <i>Conservation Biology</i> . 20(3) , 833–843. (2006).
<i>Primula vulgaris</i>	Plantae	Displays senescence		Valdés, A., García, D., García, M. B., & Ehrlén, J. Contrasting effects of different landscape

			0.290	characteristics on population growth of a perennial forest herb. <i>Ecography</i> . 37(3) , 230–240. (2013).
<i>Ramonda myconi</i>	Plantae	Escapes senescence	1.394	Xavier Picó, F., & Riba, M. <i>Plant Ecology</i> . 161(1) , 1–13. (2002).
<i>Sarcocapnos pulcherrima</i>	Plantae	Displays senescence	0.898	Salinas, M. J., Suárez, V., & Blanca, G. Demographic structure of three species of <i>Sarcocapnos</i> (<i>Fumariaceae</i>) as a basis for their conservation. <i>Canadian Journal of Botany</i> . 80(4) , 360–369. (2002).
<i>Saxifraga aizoides</i>	Plantae	Escapes senescence	1.355	Marcante, S., Winkler, E., & Erschbamer, B. Population dynamics along a primary succession gradient: do alpine species fit into demographic succession theory? <i>Annals of Botany</i> . 103(7) , 1129–1143. (2009).
<i>Saxifraga cotyledon</i>	Plantae	Escapes senescence	1.136	Dinnézt, P., & Nilsson, T. Population viability analysis of <i>Saxifraga cotyledon</i> , a perennial plant with semelparous rosettes. <i>Plant Ecology</i> . 159(1) , 61–71. (2002).
<i>Silene acaulis</i>	Plantae	Escapes senescence	1.865	Morris, W. & Doak, D. Life history of the long-lived gynodioecious cushion plant <i>Silene acaulis</i> (<i>Caryophyllaceae</i>), inferred from size-based population projection matrices. <i>Am J Bot.</i> 85(6) : 784. (1998).
<i>Silene douglasii oraria</i>	Plantae	Displays senescence	0.500	Kephart, S. R., & Paladino, C. Demographic change and microhabitat Variability in a Grassland Endemic, <i>Silene Douglasii</i> Var. <i>oraria</i> (<i>Caryophyllaceae</i>). <i>American Journal of Botany</i> . 84(2) , 179–189. (1997).
<i>Sporobolus heterolepis</i>	Plantae	Displays senescence	0.830	Dalgleish, H. J., Kula, A. R., Hartnett, D. C., & Sandercock, B. K. Responses of two bunchgrasses to nitrogen addition in tallgrass prairie: the role of bud bank demography. <i>American Journal of Botany</i> . 95(6) , 672–680. (2008).

			0.364	Jongejans, E., & De Kroon, H. Space versus time variation in the population dynamics of three co-occurring perennial herbs. <i>Journal of Ecology</i> . 93(4) , 681–692. (2005).
<i>Succisa pratensis</i>	Plantae	Displays senescence		
			0.976	Iriondo; Albert; Gimenez; Lozana; Escuerdo 978-84-8014-746-0
<i>Thymus vulgaris</i>	Plantae	Displays senescence		
			1.216	Ohara, M., Takada, T., & Kawano, S. Demography and reproductive strategies of a polycarpic perennial, <i>Trillium apetalon</i> (Trilliaceae). <i>Plant Species Biology</i> . 16(3) , 209–217. (2001).
<i>Trillium apetalon</i>	Plantae	Escapes senescence		
			0.878	Ohara, M., Tomimatsu, H., Takada, T., & Kawano, S. Importance of life history studies for conservation of fragmented populations: A case study of the understory herb, <i>Trillium camschatcense</i> . <i>Plant Species Biology</i> . 21(1) , 1–12. (2006).
<i>Trillium camschatcense</i>	Plantae	Displays senescence		
			1.394	Knight, T. M. Effects of herbivory and its timing across populations of <i>Trillium grandiflorum</i> (Liliaceae). <i>American Journal of Botany</i> . 90(8) , 1207–1214. (2003).
<i>Trillium grandiflorum</i>	Plantae	Escapes senescence		
<i>Trillium ovatum</i>	Plantae	Escapes senescence	1.485	Ream, PhD thesis, 2011.
<i>Trillium persistens</i>	Plantae	Displays senescence	0.869	Plank, MSc thesis, 2010.
			0.959	Scanga, S. E. Population dynamics in canopy gaps: nonlinear response to variable light regimes by an understory plant. <i>Plant Ecology</i> . 215(8) , 927–935. (2014).
<i>Trollius laxus</i>	Plantae	Displays senescence		
			0.734	Eckstein, R., Danihelka, J., & Otte, A. Variation in life-cycle between three rare and endangered floodplain violets in two regions: implications for population viability and conservation. <i>Biologia</i> . 64(1) . (2009).
<i>Viola pumila</i>	Plantae	Displays senescence		
				Sanchez-Velasquez, L. R., Ezcurra, E., Martinez-Ramos, M., Alvarez-Buylla, E., & Lorente, R. Population dynamics of <i>Zea diploperennis</i> , an endangered perennial herb: effect of slash and burn practice. <i>Journal of Ecology</i> .
<i>Zea diploperennis</i>	Plantae	Displays senescence		

			0.645	90(4), 684–692. (2002).
			1.646	Wong, T. M., & Ticktin, T. Using population dynamics modelling to evaluate potential success of restoration: a case study of a Hawaiian vine in a changing climate. <i>Environmental Conservation</i> . 42(1) , 20–30. (2014).
<i>Alyxia stellata</i>	Plantae	Escapes senescence		
			1.444	Nabe-Nielsen, J. Demography of <i>Machaerium cuspidatum</i> , a shade-tolerant neotropical liana. <i>Journal of Tropical Ecology</i> . 20(5) , 505–516. (2004).
<i>Machaerium cuspidatum</i>	Plantae	Escapes senescence		
			1.571	Quitete Portela, R. de C., Bruna, E. M., & Maës dos Santos, F. A. Demography of palm species in Brazil's Atlantic forest: a comparison of harvested and unharvested species using matrix models. <i>Biodiversity and Conservation</i> . 19(8) , 2389–2403. (2010).
<i>Astrocaryum aculeatissimum</i>	Plantae	Escapes senescence		
			1.561	Pinero, D., Martinez-Ramos, M., & Sarukhan, J. A Population Model of <i>Astrocaryum Mexicanum</i> and a Sensitivity Analysis of its Finite Rate of Increase. <i>The Journal of Ecology</i> . 72(3) , 977. (1984).
<i>Astrocaryum mexicanum</i>	Plantae	Escapes senescence		
			1.763	Barot, S., Gignoux, J., Vuattoux, R., & Legendre, S. Demography of a savanna palm tree in Ivory Coast (Lamto): population persistence and life-history. <i>Journal of Tropical Ecology</i> . 16(5) , 637–655. (2000).
<i>Borassus aethiopum</i>	Plantae	Escapes senescence		
			1.508	Binh, PhD thesis, 2009.
<i>Calamus nambariensis</i>	Plantae	Escapes senescence		
			1.385	Binh, PhD thesis, 2009.
<i>Calamus rhabdocladus</i>	Plantae	Escapes senescence		
			1.227	Valverde, T., Hernandez-Apolinar, M., & Mendoza-Amarom, S. Effect of Leaf Harvesting on the Demography of the Tropical Palm <i>Chamaedorea elegans</i> in South-Eastern Mexico. <i>Journal of Sustainable Forestry</i> . 23(1) , 85–105. (2006).
<i>Chamaedorea elegans</i>	Plantae	Escapes senescence		
				Olmsted, I., & Alvarez-Buylla, E. R. Sustainable Harvesting of Tropical Trees: Demography and Matrix Models of Two Palm Species in Mexico. <i>Ecological</i>
<i>Coccothrinax readii</i>	Plantae	Escapes senescence		

			2.344	<i>Applications</i> . 5(2) , 484–500. (1995).
<i>Daemonorops poilanei</i>	Plantae	Escapes senescence	1.515	Binh, PhD thesis, 2009.
<i>Dioon caputoi</i>	Plantae	Escapes senescence	1.871	Cabrera-Toledo, PhD thesis, 2009.
				Lázaro-Zermeño, J. M., González-Espinosa, M., Mendoza, A., Martínez-Ramos, M., & Quintana-Ascencio, P. F. Individual growth, reproduction and population dynamics of <i>Dioon merolae</i> (Zamiaceae) under different leaf harvest histories in Central Chiapas, Mexico. <i>Forest Ecology and Management</i> . 261(3) , 427–439. (2011).
<i>Dioon merolae</i>	Plantae	Escapes senescence	1.698	
<i>Dioon spinulosum</i>	Plantae	Escapes senescence	2.323	Casteneda MSc thesis, 2008.
				Raimondo, D. C., & Donaldson, J. S. Responses of cycads with different life histories to the impact of plant collecting: simulation models to determine important life history stages and population recovery times. <i>Biological Conservation</i> . 111(3) , 345–358. (2003).
<i>Encephalartos cycadifolius</i>	Plantae	Escapes senescence	2.935	
				Kouassi, K. I., Barot, S., Gignoux, J., & Zoro Bi, I. A. Demography and life history of two rattan species, <i>Eremospatha macrocarpa</i> and <i>Laccosperma secundiflorum</i> , in Côte d'Ivoire. <i>Journal of Tropical Ecology</i> . 24(05) , 493–503. (2008).
<i>Eremospatha macrocarpa</i>	Plantae	Escapes senescence	1.115	
				A. Arango, D., J. Duque, Á., & Muñoz, E. Dinámica poblacional de la palma <i>Euterpe oleracea</i> (Arecaceae) en bosques inundables del Chocó, Pacífico colombiano. <i>Revista de Biología Tropical</i> . 58(1) . (2009).
<i>Euterpe oleracea</i>	Plantae	Escapes senescence	1.112	
				Otárola, M. F., & Avalos, G. Demographic variation across successional stages and their effects on the population dynamics of the neotropical palm <i>Euterpe precatoria</i> . <i>American Journal of Botany</i> . 101(6) , 1023–1028. (2014).
<i>Euterpe precatoria</i>	Plantae	Escapes senescence	1.051	
<i>Geonoma pohliana</i>	Plantae	Escapes senescence		Souza, A. F., & Martins, F. R. Demography of the clonal palm

<i>weddelliana</i>				1.015	<i>Geonoma brevispatha</i> in a Neotropical swamp forest. <i>Austral Ecology</i> . 31(7) , 869–881. (2006).
<i>Geonoma macrostachys</i>	Plantae	Escapes senescence		1.618	Svenning, J.-C. Crown illumination limits the population growth rate of a neotropical understorey palm (<i>Geonoma macrostachys</i>). <i>Plant Ecology</i> . 159(2) , 185–199. (2002).
<i>Geonoma orbignyana</i>	Plantae	Escapes senescence		1.248	Rodríguez-Buriticá, S., Orjuela, M. A., & Galeano, G. Demography and life history of <i>Geonoma orbignyana</i> : An understory palm used as foliage in Colombia. <i>Forest Ecology and Management</i> . 211(3) , 329–340. (2005).
<i>Geonoma schottiana</i>	Plantae	Escapes senescence		1.889	Sampaio, M. B., & Scariot, A. Effects of stochastic herbivory events on population maintenance of an understorey palm species (<i>Geonoma schottiana</i>) in riparian tropical forest. <i>Journal of Tropical Ecology</i> . 26(2) , 151–161. (2010).
<i>Iriartea deltoidea</i>	Plantae	Escapes senescence		1.304	Pinard, M. Impacts of Stem Harvesting on Populations of <i>Iriartea deltoidea</i> (Palmae) in an Extractive Reserve in Acre, Brazil. <i>Biotropica</i> . 25(1) , 2. (1993).
<i>Mauritia flexuosa</i>	Plantae	Escapes senescence		1.707	Holm, J. A., Miller, C. J., & Cropper, W. P. Population Dynamics of the Dioecious Amazonian Palm <i>Mauritia flexuosa</i> : Simulation Analysis of Sustainable Harvesting. <i>Biotropica</i> . 40(5) , 550–558. (2008).
<i>Dypsis decaryi</i>	Plantae	Escapes senescence		2.000	Ratsirarson, J., Silander, J. A., & Richard, A. F. Conservation and Management of a Threatened Madagascar Palm Species, <i>Neodypsis decaryi</i> , Jumelle. <i>Conservation Biology</i> . 10(1) , 40–52. (1996).
<i>Phytelephas seemannii</i>	Plantae	Escapes senescence		2.024	Bernal, R. Demography of the vegetable ivory palm <i>Phytelephas seemannii</i> in Colombia, and the impact of seed harvesting. <i>Journal of Applied Ecology</i> . 35(1) , 64–74. (1998).
<i>Podococcus barteri</i>	Plantae	Displays senescence			Bullock, S. H. Demography of an Undergrowth Palm in Littoral

			0.865	Cameroon. <i>Biotropica</i> . 12(4) , 247. (1980).
<i>Pseudophoenix sargentii</i>	Plantae	Escapes senescence	1.695	Duran; Franco, PhD thesis, 1992.
<i>Rhopalostylis sapida</i>	Plantae	Displays senescence	0.648	Enright, N. J., & Watson, A. D. Population dynamics of the nikau palm, <i>Rhopalostylis sapida</i> (Wendl. et Drude), in a temperate forest remnant near Auckland, New Zealand. <i>New Zealand Journal of Botany</i> . 30(1) , 29–43. (1992).
<i>Sabal yapa</i>	Plantae	Escapes senescence	1.656	Pulido, M. T., Valverde, T., & Caballero, J. Variation in the population dynamics of the palm <i>Sabal yapa</i> in a landscape shaped by shifting cultivation in the Yucatan Peninsula, Mexico. <i>Journal of Tropical Ecology</i> . 23(2) , 139–149. (2007).
<i>Thrinax radiata</i>	Plantae	Escapes senescence	1.936	Olmsted, I., & Alvarez-Buylla, E. R. Sustainable Harvesting of Tropical Trees: Demography and Matrix Models of Two Palm Species in Mexico. <i>Ecological Applications</i> . 5(2) , 484–500. (1995).
<i>Ardisia elliptica</i>	Plantae	Escapes senescence	2.388	Koop, A. L., & Horvitz, C. C. Projection matrix analysis of the demography of an invasive, non-native shrub (<i>Ardisia elliptica</i>). <i>Ecology</i> , 86(10) , 2661–2672. (2005).
<i>Argyroxiphium sandwicense</i>	Plantae	Escapes senescence	1.317	Forsyth, S. A. Density-dependent seed set in the Haleakala silversword: evidence for an Allee effect. <i>Oecologia</i> . 136(4) , 551–557. (2003).
<i>Atriplex acanthocarpa</i>	Plantae	Displays senescence	0.797	Verhulst, J., Montaña, C., Mandujano, M. C., & Franco, M. Demographic mechanisms in the coexistence of two closely related perennials in a fluctuating environment. <i>Oecologia</i> . 156(1) , 95–105. (2008).
<i>Banksia ericifolia</i>	Plantae	Escapes senescence	1.088	Bradstock, R. A., & O'Connell, M. A. (1988). Demography of woody plants in relation to fire: <i>Banksia ericifolia</i> L.f. and <i>Petrophile pulchella</i> (Schrad) R.Br. <i>Austral Ecology</i> . 13(4) , 505–518. (1988).
<i>Cassia nemophila</i>	Plantae	Escapes senescence		Silander, J. A. Demographic variation in the Australian desert

			1.881	cassia under grazing pressure. <i>Oecologia</i> . 60(2) , 227–233. (1983).
<i>Cytisus scoparius</i>	Plantae	Escapes senescence	1.334	Neubert, M. G., & Parker, I. M. Projecting Rates of Spread for Invasive Species. <i>Risk Analysis</i> . 24(4) , 817–831. (2004).
<i>Daphne rodriguezii</i>	Plantae	Escapes senescence	1.156	Rodríguez-Pérez, J., & Traveset, A. Demographic consequences for a threatened plant after the loss of its only disperser. Habitat suitability buffers limited seed dispersal. <i>Oikos</i> . 121(6) , 835–847. (2011).
<i>Fumana procumbens</i>	Plantae	Escapes senescence	1.032	Bengtsson, K. <i>Fumana Procumbens</i> on Oland--Population Dynamics of a Disjunct Species at the Northern Limit of its Range. <i>The Journal of Ecology</i> . 81(4) , 745. (1993).
<i>Helianthemum juliae</i>	Plantae	Displays senescence	0.946	Marrero-Gómez, M. V., Oostermeijer, J. G. B., Carqué-Álamo, E., & Bañares-Baudet, Á. Population viability of the narrow endemic <i>Helianthemum juliae</i> (CISTACEAE) in relation to climate variability. <i>Biological Conservation</i> . 136(4) , 552–562. (2007).
<i>Lindera umbellata</i>	Plantae	Escapes senescence	1.421	Hara, M., Kanno, H., Hirabuki, Y., & Takehara, A. Population dynamics of four understory shrub species in beech forest. <i>Journal of Vegetation Science</i> . 15(4) , 475–484. (2004).
<i>Linnaea borealis</i>	Plantae	Displays senescence	0.634	Eriksson, O. Population structure and dynamics of the clonal dwarf-shrub <i>Linnaea borealis</i> . <i>Journal of Vegetation Science</i> . 3(1) , 61–68. (1992).
<i>Magnolia salicifolia</i>	Plantae	Escapes senescence	1.770	Hara, M., Kanno, H., Hirabuki, Y., & Takehara, A. Population dynamics of four understory shrub species in beech forest. <i>Journal of Vegetation Science</i> . 15(4) , 475–484. (2004).
<i>Miconia albicans</i>	Plantae	Escapes senescence	1.939	Hoffmann, W. A. Fire and population dynamics of four understory shrub species in beech forest. <i>Ecology</i> . 80(4) , 1354–1369. (1999).
<i>Paliurus ramosissimus</i>	Plantae	Displays senescence		Ishihama, F., Fujii, S., Yamamoto, K., & Takada, T. Estimation of dieback process

			0.986	caused by herbivory in an endangered root-sprouting shrub species, <i>Paliurus ramosissimus</i> (Lour.) Poir., using a shoot-dynamics matrix model. <i>Population Ecology</i> . 56(2) , 275–288. (2013).
<i>Persoonia glaucescens</i>	Plantae	Escapes senescence	1.061	McKenna, PhD thesis, 2007.
<i>Purshia subintegra</i>	Plantae	Displays senescence	0.523	Maschinski, J., Baggs, J. E., Quintana-Ascencio, P. F., & Menges, E. S. Using Population Viability Analysis to Predict the Effects of Climate Change on the Extinction Risk of an Endangered Limestone Endemic Shrub, Arizona Cliffrose. <i>Conservation Biology</i> . 20(1) , 218–228. (2006).
<i>Rhododendron maximum</i>	Plantae	Displays senescence	0.546	McGraw, J. B. Effects of age and size on life histories and population growth of <i>Rhododendron maximum</i> shoots. <i>American Journal of Botany</i> . 76(1) , 113–123. (1989).
<i>Rhus copallinum</i>	Plantae	Displays senescence	0.506	Thaxton, PhD thesis, 2003.
<i>Rourea induta</i>	Plantae	Escapes senescence	1.362	Hoffmann, W. A. Fire and population dynamics of four understorey shrub species in beech forest. <i>Ecology</i> . 80(4) , 1354–1369. (1999).
<i>Verticordia staminosa</i>	Plantae	Displays senescence	0.775	Yates, C. J., Ladd, P. G., Coates, D. J., & McArthur, S. Hierarchies of cause: understanding rarity in an endemic shrub <i>Verticordia staminosa</i> (Myrtaceae) with a highly restricted distribution. <i>Australian Journal of Botany</i> . 55(3) , 194. (2007).
<i>Viburnum furcatum</i>	Plantae	Escapes senescence	1.925	Hara, M., Kanno, H., Hirabuki, Y., & Takehara, A. Population dynamics of four understorey shrub species in beech forest. <i>Journal of Vegetation Science</i> . 15(4) , 475–484. (2004).
<i>Astrophytum asterias</i>	Plantae	Displays senescence	0.960	Martinez-Avalos, PhD thesis, 2007.
<i>Astrophytum capricorne</i>	Plantae	Displays senescence	0.468	Bravo Espinoza, PhD thesis, 2011.
<i>Astrophytum ornatum</i>	Plantae	Escapes senescence	1.270	V Zepeda-Martínez, MC Mandujano, FJ Mandujano, JK Golubov. What can the demography of <i>Astrophytum ornatum</i> tell us of its endangered status? <i>Journal of arid</i>

<i>Cephalocereus senilis</i>	Plantae	Displays senescence	0.947	<i>environments</i> . 88 , 244-249. (2013). Cedillo Castillo, MSc thesis, 2007.
<i>Echinocactus platyacanthus</i>	Plantae	Escapes senescence	2.021	Jiménez-Sierra, C., Mandujano, M. C., & Eguiarte, L. E. Are populations of the candy barrel cactus (<i>Echinocactus platyacanthus</i>) in the desert of Tehuacán, Mexico at risk? Population projection matrix and life table response analysis. <i>Biological Conservation</i> . 135(2) , 278–292. (2007).
<i>Escontria chiotilla</i>	Plantae	Escapes senescence	1.260	Ortega-Baes, PhD thesis, 2001.
<i>Coespeletia timotensis</i>	Plantae	Displays senescence	0.397	Silva, J. F., Trevisan, M. C., Estrada, C. A., & Monasterio, M. Comparative demography of two giant caulescent rosettes (<i>Espeletia timotensis</i> and <i>E. spicata</i>) from the high tropical Andes. <i>Global Ecology and Biogeography</i> . 9(5) , 403–413. (2000).
<i>Harrisia fragrans</i>	Plantae	Escapes senescence	1.595	Rae, J. G., & Ebert, T. A. Demography of the Endangered Fragrant Prickly Apple Cactus, <i>Harrisia fragrans</i> . <i>International Journal of Plant Sciences</i> . 163(4) , 631–640. (2002).
<i>Mammillaria crucigera</i>	Plantae	Displays senescence	0.060	Contreras, C., & Valverde, T. Evaluation of the conservation status of a rare cactus (<i>Mammillaria crucigera</i>) through the analysis of its population dynamics. <i>Journal of Arid Environments</i> . 51(1) , 89–102. (2002).
<i>Mammillaria hernandezii</i>	Plantae	Escapes senescence	1.788	Rodriguez Ortega, PhD thesis, 2008.
<i>Mammillaria huitzilopochtli</i>	Plantae	Escapes senescence	1.263	Martinez, A-F., Medina, G.I.M., Golubov, J., Montana, C. & Mandujano, M.C. Demography of an endangered epidemic rupicolous cactus. <i>Plant Ecology</i> . 210 , 53-66 (2010).
<i>Mammillaria magnimamma</i>	Plantae	Escapes senescence	1.663	Valverde, T., Quijas, S., López-Villavicencio, M., & Castillo, S. Population dynamics of <i>Mammillaria magnimamma</i> (Cactaceae) in a lava-field in central Mexico. <i>Plant Ecology (formerly Vegetatio)</i> . 170(2) ,

				167–184. (2004).
<i>Mammillaria mystax</i>	Plantae	Displays senescence	0.719	Saldivar Sanches, Navarro Carbajal, Cact Suc Mex, 2012.
<i>Mammillaria napina</i>	Plantae	Escapes senescence	1.802	Rodriguez Ortega, PhD thesis, 2008.
<i>Mammillaria pectinifera</i>	Plantae	Escapes senescence	1.039	Valverde, P.L. & Zavala-Hurtado, J.A. Assessing the ecological status of <i>Mammillaria pectinifera</i> Weber (cactaceae), a rare and threatened species endemic of the Tehuacan-Cuitcatlan Region in Central Mexico. <i>Journal of Arid Environments</i> . 64(2) 193-208 (2006).
<i>Mammillaria supertexta</i>	Plantae	Escapes senescence	1.069	Avendano Calco, MSc thesis, 2007.
<i>Neobuxbaumia macrocephala</i>	Plantae	Escapes senescence	1.193	Esparza-Olguin, L., Valverde, T. & Mandujano, M.C. Comparative demographic analysis of three <i>Neobuxbaumia</i> species (cactaceae) with differing degree of rarity. <i>Population Ecology</i> . 47(3) 229-245 (2005).
<i>Neobuxbaumia mezcalaensis</i>	Plantae	Escapes senescence	1.849	Esparza-Olguin, L., Valverde, T. & Mandujano, M.C. Comparative demographic analysis of three <i>Neobuxbaumia</i> species (cactaceae) with differing degree of rarity. <i>Population Ecology</i> . 47(3) 229-245 (2005).
<i>Neobuxbaumia polylopha</i>	Plantae	Escapes senescence	1.691	Arroyo-Cosultchi, G., Golubov, J. & Mandujano, M.C. Pulse seedling recruitment on the population dynamics of a columnar cactus: Effect of an extreme rainfall event. <i>Acta Oecologica</i> . 71 , 52-60 (2016)
<i>Neobuxbaumia tetetzo</i>	Plantae	Escapes senescence	2.550	Esparza-Olguin, L., Valverde, T. & Mandujano, M.C. Comparative demographic analysis of three <i>Neobuxbaumia</i> species (cactaceae) with differing degree of rarity. <i>Population Ecology</i> . 47(3) 229-245 (2005).
<i>Opuntia macrocentra</i>	Plantae	Escapes senescence	1.068	Mandujano, M. C., Golubov, J., & Huenneke, L. F. Effect of reproductive modes and environmental heterogeneity in the population dynamics of a geographically widespread clonal desert cactus. <i>Population Ecology</i> . 49(2) , 141–153. (2007).

<i>Opuntia macrorhiza</i>	Plantae	Displays senescence	0.839	Haridas, C. V., Keeler, K. H., & Tenhumberg, B. Variation in the local population dynamics of the short-lived <i>Opuntia macrorhiza</i> (Cactaceae). <i>Ecology</i> . 96 (3), 800–807. (2015).
<i>Opuntia microdasys</i>	Plantae	Escapes senescence	1.491	Carrillo Angeles, PhD thesis, 2011.
<i>Opuntia rastrera</i>	Plantae	Escapes senescence	1.692	Mandujano, M. C., Montaña, C., Franco, M., Golubov, J., & Flores-Martínez, A. Integration of demographic annual variability in a clonal desert cactus. <i>Ecology</i> . 82 (2), 344–359. (2001).
<i>Abies concolor</i>	Plantae	Escapes senescence	1.258	Van Mantgem, P.J. & Stephenson, N.L. The accuracy of matrix population models for coniferous trees in the Sierra Nevada, California. <i>Journal of Ecology</i> . 93 (4), 737-747 (2005)
<i>Abies magnifica</i>	Plantae	Escapes senescence	1.172	Van Mantgem, P.J. & Stephenson, N.L. The accuracy of matrix population models for coniferous trees in the Sierra Nevada, California. <i>Journal of Ecology</i> . 93 (4), 737-747 (2005)
<i>Abies sachalinensis</i>	Plantae	Displays senescence	0.912	Hiura, T., & Fujiwara, K. Density-dependence and co-existence of conifer and broad-leaved trees in a Japanese northern mixed forest. <i>Journal of Vegetation Science</i> . 10 (6), 843–850. (1999).
<i>Acer palmatum</i>	Plantae	Escapes senescence	2.191	Tanaka, H. <i>et al.</i> Comparative demography of three coexisting Acer species in gaps and under closed canopy. <i>Journal of Vegetation Science</i> . 19 (1), 127–138. (2008).
<i>Acer pictum</i>	Plantae	Escapes senescence	1.476	Tanaka, H. <i>et al.</i> Comparative demography of three coexisting Acer species in gaps and under closed canopy. <i>Journal of Vegetation Science</i> . 19 (1), 127–138. (2008).
<i>Acer rufinerve</i>	Plantae	Escapes senescence	1.984	Tanaka, H. <i>et al.</i> Comparative demography of three coexisting Acer species in gaps and under closed canopy. <i>Journal of Vegetation Science</i> . 19 (1), 127–138. (2008).
<i>Aesculus turbinata</i>	Plantae	Escapes senescence	2.265	Kaneko, Y., Takada, T. & Kawana, S. Population biology of <i>Aesculus turbinata</i> : A

				demographic analysis using transition matrices on a natural population along a riparian environmental gradient. <i>Plant Species Biology</i> . 14(1) , 47-68. (1999).
<i>Ailanthus altissima</i>	Plantae	Escapes senescence	1.066	Burns, J. H. <i>et al.</i> Greater sexual reproduction contributes to differences in demography of invasive plants and their non-invasive relatives. <i>Ecology</i> . 94(5) , 995–1004. (2013).
<i>Alnus incana rugosa</i>	Plantae	Escapes senescence	1.186	Huenneke, L. F., & Marks, P. L. Stem Dynamics of the Shrub <i>Alnus Incana</i> SSP. Rugosa: Transition Matrix Models. <i>Ecology</i> . 68(5) , 1234–1242. (1987).
<i>Aquilaria crassna</i>	Plantae	Escapes senescence	1.376	Zhang, L., Brockelman, W. Y., & Allen, M. A. Matrix analysis to evaluate sustainability: The tropical tree <i>Aquilaria crassna</i> , a heavily poached source of agarwood. <i>Biological Conservation</i> . 141(6) , 1676–1686. (2008).
<i>Aquilaria malaccensis</i>	Plantae	Displays senescence	0.292	Soehartono, T., & C. Newton, A. Conservation and sustainable use of tropical trees in the genus <i>Aquilaria</i> II. The impact of gaharu harvesting in Indonesia. <i>Biological Conservation</i> . 97(1) , 29–41. (2001).
<i>Aquilaria microcarpa</i>	Plantae	Displays senescence	0.568	Soehartono, T., & C. Newton, A. Conservation and sustainable use of tropical trees in the genus <i>Aquilaria</i> II. The impact of gaharu harvesting in Indonesia. <i>Biological Conservation</i> . 97(1) , 29–41. (2001).
<i>Araucaria hunsteinii</i>	Plantae	Escapes senescence	2.839	Enright, N. J. Does <i>Araucaria hunsteinii</i> compete with its neighbours? <i>Austral Ecology</i> . 7(1) , 97–99. (1982).
<i>Araucaria muelleri</i>	Plantae	Escapes senescence	1.042	Enright, N. J., Miller, B. P., Perry, G. L. W., Goldblum, D., & Jaffré, T. Stress-tolerator leaf traits determine population dynamics in the endangered New Caledonian conifer <i>Araucaria muelleri</i> . <i>Austral Ecology</i> . 39(1) , 60–71. (2013).
<i>Avicennia germinans</i>	Plantae	Escapes senescence	2.314	Lopez-Hoffman, L., Ackerley, D. D., Aanten, N. P. R., Denoyer, J.

<i>Bertholletia excelsa</i>	Plantae	Escapes senescence	3.151	L., & Martinez-Ramos, M. Gap-dependence in mangrove life-history strategies: a consideration of the entire life cycle and patch dynamics. <i>Journal of Ecology</i> . 95(6) , 1222–1233. (2007). Zuidema, P. A., & Boot, R. G. A. Demography of the Brazil nut tree (<i>Bertholletia excelsa</i>) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics. <i>Journal of Tropical Ecology</i> . 18(1) , 1–31. (2002).
<i>Boswellia papyrifera</i>	Plantae	Escapes senescence	1.410	Groenendijk, P., Eshete, A., Sterck, F. J., Zuidema, P. A., & Bongers, F. Limitations to sustainable frankincense production: blocked regeneration, high adult mortality and declining populations. <i>Journal of Applied Ecology</i> . 49(1) , 164–173. (2011).
<i>Brosimum alicastrum</i>	Plantae	Displays senescence	0.201	Peters, PhD thesis, 1989.
<i>Bursera glabrifolia</i>	Plantae	Escapes senescence	2.262	Hernández-Apolinar, M., Valverde, T., & Purata, S. Demography of <i>Bursera glabrifolia</i> , a tropical tree used for folk woodcrafting in Southern Mexico: An evaluation of its management plan. <i>Forest Ecology and Management</i> . 223(1-3) , 139–151. (2006).
<i>Calocedrus decurrens</i>	Plantae	Escapes senescence	1.583	Van Mantgem, P. J., & Stephenson, N. L. The accuracy of matrix population model projections for coniferous trees in the Sierra Nevada, California. <i>Journal of Ecology</i> . 93(4) , 737–747. (2005).
<i>Calocedrus macrolepis</i>	Plantae	Escapes senescence	1.201	Chien, P. D., Zuidema, P. A., & Nghia, N. H. Conservation prospects for threatened Vietnamese tree species: results from a demographic study. <i>Population Ecology</i> . 50(2) , 227–237. (2008).
<i>Camellia japonica</i>	Plantae	Escapes senescence		Shimatani, I.K., Kubota, Y., Araki, K., Aikawa, S-I. & Manabe, T. Matrix models using fine size classes and their application to the population

			2.147	dynamics of tree species: Bayesian non-parametric estimation. <i>Plant Spp Biol.</i> 22(3) , 175-190. (2007)
<i>Castanea dentata</i>	Plantae	Escapes senescence	1.987	Davelos, A. L., & Jarosz, A. M. Demography of American chestnut populations: effects of a pathogen and a hyperparasite. <i>Journal of Ecology.</i> 92(4) , 675–685. (2004).
<i>Cecropia obtusifolia</i>	Plantae	Displays senescence	0.004	Alvarez-Buylla, E. R. Density Dependence and Patch Dynamics in Tropical Rain Forests: Matrix Models and Applications to a Tree Species. <i>Am.Nat.</i> 143(1) , 155–191. (1994).
<i>Choerospondias axillaris</i>	Plantae	Displays senescence	0.045	Brodie, J. F., Helmy, O. E., Brockelman, W. Y., & Maron, J. L. Functional differences within a guild of tropical mammalian frugivores. <i>Ecology.</i> 90(3) , 688–698. (2009).
<i>Dacrydium elatum</i>	Plantae	Escapes senescence	1.671	Chien, P. D., Zuidema, P. A., & Nghia, N. H. Conservation prospects for threatened Vietnamese tree species: results from a demographic study. <i>Population Ecology.</i> 50(2) , 227–237. (2008).
<i>Dicorynia guianensis</i>	Plantae	Displays senescence	0.709	Picard, N., Ouédraogo, D., & Bar-Hen, A. Choosing classes for size projection matrix models. <i>Ecological Modelling.</i> 221(19) , 2270–2279. (2010).
<i>Dicymbe altsonii</i>	Plantae	Escapes senescence	2.731	Zagt;Boot PhD thesis, 1997.
<i>Duguetia neglecta</i>	Plantae	Escapes senescence	2.301	Zagt;Boot PhD thesis, 1997.
<i>Eperua falcata</i>	Plantae	Displays senescence	0.778	Chagneau, P., Mortier, F., & Picard, N. (2009). Designing permanent sample plots by using a spatially hierarchical matrix population model. <i>Journal of the Royal Statistical Society: Series C (Applied Statistics).</i> 58(3) , 345–367. (2009).
<i>Fagus grandifolia</i>	Plantae	Escapes senescence	1.285	Batista, W. B., Platt, W. J., & Macchiavelli, R. E. Demography of a Shade-Tolerant Tree (<i>Fagus grandifolia</i>) in a Hurricane-Disturbed Forest. <i>Ecology.</i> 79(1) , 38. (1998).
<i>Grias peruviana</i>	Plantae	Escapes senescence	1.176	Peters, <i>Ecol & Manag Non-timber Forest Resources</i> , 1995.
<i>Guaiacum</i>	Plantae	Escapes senescence	2.145	CITES, Plants Committee, 2008.

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<i>Guettarda viburnoides</i>	Plantae	Displays senescence	0.429	Loayza, A. P., & Knight, T. Seed dispersal by pulp consumers, not “legitimate” seed dispersers, increases <i>Guettarda viburnoides</i> population growth. <i>Ecology</i> . 91(9) , 2684–2695. (2010).
<i>Himatanthus drasticus</i>	Plantae	Escapes senescence	1.006	Baldauf, C., Corrêa, C. E., Ferreira, R. C., & dos Santos, F. A. M. Assessing the effects of natural and anthropogenic drivers on the demography of <i>Himatanthus drasticus</i> (Apocynaceae): Implications for sustainable management. <i>Forest Ecology and Management</i> . 354 , 177–184. (2015).
<i>Juniperus procera</i>	Plantae	Escapes senescence	2.455	Couralet, C., Sass-Klaassen, U., Sterck, F., Bekele, T., & Zuidema, P. A. Combining dendrochronology and matrix modelling in demographic studies: An evaluation for <i>Juniperus procera</i> in Ethiopia. <i>Forest Ecology and Management</i> . 216(1-3) , 317–330. (2005).
<i>Khaya senegalensis</i>	Plantae	Escapes senescence	1.370	Gaoue, O. G., & Ticktin, T. Effects of Harvest of Nontimber Forest Products and Ecological Differences between Sites on the Demography of African Mahogany. <i>Conservation Biology</i> . 24(2) , 605–614. (2010).
<i>Magnolia macrophylla dealbata</i>	Plantae	Escapes senescence	1.484	Sánchez-Velásquez, L. R., & Pineda-López, M. del R. Comparative demographic analysis in contrasting environments of <i>Magnolia dealbata</i> : an endangered species from Mexico. <i>Population Ecology</i> . 52(1) , 203–210. (2009).
<i>Magnolia fordiana</i>	Plantae	Escapes senescence	1.106	Chien, P. D., Zuidema, P. A., & Nghia, N. H. Conservation prospects for threatened Vietnamese tree species: results from a demographic study. <i>Population Ecology</i> . 50(2) , 227–237. (2008).
<i>Microberlinia bisulcata</i>	Plantae	Escapes senescence	2.749	Norghauer, J. M., & Newbery, D. M. Seed fate and seedling dynamics after masting in two African rain forest trees. <i>Ecological Monographs</i> . 81(3) , 443–469. (2011).

<i>Parashorea chinensis</i>	Plantae	Escapes senescence	1.545	Chien, P. D., Zuidema, P. A., & Nghia, N. H. Conservation prospects for threatened Vietnamese tree species: results from a demographic study. <i>Population Ecology</i> . 50(2) , 227–237. (2008).
<i>Parkinsonia aculeata</i>	Plantae	Displays senescence	0.334	Raghu, S., Wilson, J. R., & Dhileepan, K. Refining the process of agent selection through understanding plant demography and plant response to herbivory. <i>Australian Journal of Entomology</i> . 45(4) , 308–316. (2006).
<i>Pentaclethra macroloba</i>	Plantae	Escapes senescence	1.147	Hartshorn, PhD thesis, 1972.
<i>Phyllanthus emblica</i>	Plantae	Escapes senescence	1.142	Ellis, M. M. <i>et al.</i> Matrix population models from 20 studies of perennial plant populations. <i>Ecology</i> . 93(4) , 951–951. (2012).
<i>Phyllanthus indofischeri</i>	Plantae	Escapes senescence	1.370	Ticktin, T., Ganesan, R., Paramesha, M., & Setty, S. Disentangling the effects of multiple anthropogenic drivers on the decline of two tropical dry forest trees. <i>Journal of Applied Ecology</i> . 49(4) , 774–784. (2012).
<i>Pinus fenzeliana</i>	Plantae	Escapes senescence	1.720	Chien, P. D., Zuidema, P. A., & Nghia, N. H. Conservation prospects for threatened Vietnamese tree species: results from a demographic study. <i>Population Ecology</i> . 50(2) , 227–237. (2008).
<i>Pinus lambertiana</i>	Plantae	Escapes senescence	1.248	Van Mantgem, P. J., & Stephenson, N. L. The accuracy of matrix population model projections for coniferous trees in the Sierra Nevada, California. <i>Journal of Ecology</i> . 93(4) , 737–747. (2005).
<i>Manilkara zapota</i>	Plantae	Escapes senescence	1.481	Cruz-Rodríguez, J. A., López-Mata, L., & Valverde, T. A comparison of traditional elasticity and variance-standardized perturbation analyses: a case study with the tropical tree species <i>Manilkara zapota</i> (Sapotaceae). <i>Journal of Tropical Ecology</i> . 25(2) , 135–146. (2009).

<i>Pinus maximartinezii</i>	Plantae	Escapes senescence	2.440	López-Mata, L. The impact of seed extraction on the population dynamics of <i>Pinus maximartinezii</i> . <i>Acta Oecologica</i> , 49 , 39–44. (2013).
<i>Pinus nigra</i>	Plantae	Escapes senescence	1.780	Buckley, Y. M. <i>et al.</i> Slowing down a pine invasion despite uncertainty in demography and dispersal. <i>Journal of Applied Ecology</i> . 42(6) , 1020–1030. (2005).
<i>Pinus ponderosa</i>	Plantae	Escapes senescence	1.034	Buckley, Y. M. <i>et al.</i> Slowing down a pine invasion despite uncertainty in demography and dispersal. <i>Journal of Applied Ecology</i> . 42(6) , 1020–1030. (2005).
<i>Pinus strobus</i>	Plantae	Escapes senescence	2.661	Münzbergová, Z., Hadincová, V., Wild, J., & Kindlmannová, J. (2013). Variability in the Contribution of Different Life Stages to Population Growth as a Key Factor in the Invasion Success of <i>Pinus strobus</i> . <i>PLoS ONE</i> . 8(2) , e56953. (2013).
<i>Pinus sylvestris</i>	Plantae	Displays senescence	0.375	Usher, M. B. A Matrix Approach to the Management of Renewable Resources, with Special Reference to Selection Forests. <i>The Journal of Applied Ecology</i> . 3(2) , 355. (1966).
<i>Prosopis flexuosa</i>	Plantae	Escapes senescence	2.249	Aschero, V., Morris, W. F., Vázquez, D. P., Alvarez, J. A., & Villagra, P. E. Demography and population growth rate of the tree <i>Prosopis flexuosa</i> with contrasting grazing regimes in the Central Monte Desert. <i>Forest Ecology and Management</i> . 369 , 184–190. (2016).
<i>Prunus africana</i>	Plantae	Displays senescence	0.150	Stewart, PhD thesis, 2001.
<i>Prunus serotina</i>	Plantae	Displays senescence	0.440	Sebert-Cuvillier, E. <i>et al.</i> Local population dynamics of an invasive tree species with a complex life-history cycle: A stochastic matrix model. <i>Ecological Modelling</i> . 201(2) , 127–143. (2007).
<i>Pterocarpus angolensis</i>	Plantae	Escapes senescence	1.770	Desmet, P.G., Shackleton, C.M. & Robinson, E.R. The population dynamics and life-history attributes of a <i>Pterocarpus angolensis</i> population in the Northern Province, South Africa.

<i>Quercus rugosa</i>	Plantae	Escapes senescence	1.698	South African <i>Journal of Botany</i> . 62(3) 160-166. (1996). Bonil; Valverde (unpublished).
<i>Rhizophora mangle</i>	Plantae	Displays senescence	0.405	Lopez Hoffman, L., Ackerly, D. D., Anten, N. P. R., Denoyer, J. L., & Martinez-Ramos, M. (2007). Gap-dependence in mangrove life-history strategies: a consideration of the entire life cycle and patch dynamics. <i>Journal of Ecology</i> . 95(6) , 1222–1233. (2007).
<i>Rhododendron ponticum</i>	Plantae	Escapes senescence	1.332	Salguero-Gomez, MSc thesis, 2004.
<i>Scaphium macropodum</i>	Plantae	Escapes senescence	1.127	Yamada, T. <i>et al.</i> Strong habitat preference of a tropical rain forest tree does not imply large differences in population dynamics across habitats. <i>Journal of Ecology</i> . 95(2) , 332–342. (2007).
<i>Shorea acuminata</i>	Plantae	Escapes senescence	1.168	Yamada, T., Yamada, Y., Okuda, T., & Fletcher, C. Soil-related variations in the population dynamics of six dipterocarp tree species with strong habitat preferences. <i>Oecologia</i> . 172(3) , 713–724. (2012).
<i>Shorea bracteolata</i>	Plantae	Escapes senescence	1.064	Yamada, T., Yamada, Y., Okuda, T., & Fletcher, C. Soil-related variations in the population dynamics of six dipterocarp tree species with strong habitat preferences. <i>Oecologia</i> . 172(3) , 713–724. (2012).
<i>Shorea leprosula</i>	Plantae	Escapes senescence	1.465	Yamada, T., Yamada, Y., Okuda, T., & Fletcher, C. Soil-related variations in the population dynamics of six dipterocarp tree species with strong habitat preferences. <i>Oecologia</i> . 172(3) , 713–724. (2012).
<i>Shorea maxwelliana</i>	Plantae	Escapes senescence	1.010	Yamada, T., Yamada, Y., Okuda, T., & Fletcher, C. Soil-related variations in the population dynamics of six dipterocarp tree species with strong habitat preferences. <i>Oecologia</i> . 172(3) , 713–724. (2012).
<i>Shorea ovalis</i>	Plantae	Escapes senescence		Yamada, T., Yamada, Y., Okuda, T., & Fletcher, C. Soil-related variations in the population

			1.072	dynamics of six dipterocarp tree species with strong habitat preferences. <i>Oecologia</i> , 172 (3), 713–724. (2012).
<i>Stryphnodendron microstachyum</i>	Plantae	Escapes senescence	2.009	Hartshorn, PhD thesis, 1972.
<i>Styrax obassis</i>	Plantae	Escapes senescence	1.443	Abe, S., Nakashizuka, T., & Tanaka, H. Effects of canopy gaps on the demography of the subcanopy tree <i>Styrax obassis</i> . <i>Journal of Vegetation Science</i> , 9 (6), 787–796. (1998).
<i>Swietenia macrophylla</i>	Plantae	Escapes senescence	1.325	Verwer, C., Peña-Claros, M., van der Staak, D., Ohlson-Kiehn, K., & Sterck, F. J. (2008). Silviculture enhances the recovery of overexploited mahogany <i>Swietenia macrophylla</i> . <i>Journal of Applied Ecology</i> , 45 (6), 1770–1779. (2008).
<i>Syzygium jambos</i>	Plantae	Escapes senescence	1.176	Brown, K. A., Spector, S., & Wu, W. Multi-scale analysis of species introductions: combining landscape and demographic models to improve management decisions about non-native species. <i>Journal of Applied Ecology</i> , 45 (6), 1639–1648. (2008).
<i>Taxus floridana</i>	Plantae	Displays senescence	0.372	Kwit, C., Horvitz, C. C., & Platt, W. J. Conserving Slow-Growing, Long-Lived Tree Species: Input from the Demography of a Rare Understory Conifer, <i>Taxus floridana</i> . <i>Conservation Biology</i> , 18 (2), 432–443. (2004).
<i>Tetraberlinia bifoliolata</i>	Plantae	Escapes senescence	1.452	Norghauer, J. M., & Newbery, D. M. Seed fate and seedling dynamics after mast in two African rain forest trees. <i>Ecological Monographs</i> , 81 (3), 443–469. (2011).
<i>Tsuga canadensis</i>	Plantae	Escapes senescence	1.378	Lamar, W. R., & McGraw, J. B. Evaluating the use of remotely sensed data in matrix population modeling for eastern hemlock (<i>Tsuga canadensis</i> L.). <i>Forest Ecology and Management</i> , 212 (1-3), 50–64. (2005).
<i>Vatica mangachapoi</i>	Plantae	Displays senescence	0.278	Hu; Wang. <i>Acta Ecol Sin.</i> (1988).

<i>Vochysia ferruginea</i>	Plantae	Displays senescence	0.641	Boucher, D. H., & Mallona, M. A. Recovery of the rain forest tree <i>Vochysia ferruginea</i> over 5 years following Hurricane Joan in Nicaragua: a preliminary population projection matrix. <i>Forest Ecology and Management</i> , 91(2-3) , 195–204. (1997).
<i>Astragalus bibullatus</i>	Plantae	Displays senescence	0.157	Bernardo, H. L., Albrecht, M. A., & Knight, T. M. Increased drought frequency alters the optimal management strategy of an endangered plant. <i>Biological Conservation</i> . 203 , 243-251. (2016).
<i>Centaurea corymbosa</i>	Plantae	Displays senescence	0.456	Hadjou Belaid, A. <i>et al.</i> Predicting population viability of the narrow endemic Mediterranean plant <i>Centaurea corymbosa</i> under climate change. <i>Biological Conservation</i> . 223 , 19-33. (2018).
<i>Melocatus bahiensis</i>	Plantae	Escapes senescence	1.195	Hughes, F. M., Figueira, J. E. C., Jacobi, C. M., & Borba, E. L. Demographic processes and anthropogenic threats of lithophytic cacti in eastern Brazil. <i>Brazilian Journal of Botany</i> . 41(3) , 631-640. (2018).
<i>Melocatus ernestii</i>	Plantae	Escapes senescence	1.496	Hughes, F. M., Figueira, J. E. C., Jacobi, C. M., & Borba, E. L. Demographic processes and anthropogenic threats of lithophytic cacti in eastern Brazil. <i>Brazilian Journal of Botany</i> . 41(3) , 631-640. (2018).
<i>Verticordia fimbriolepis</i>	Plantae	Displays senescence	0.640	Yates, C. J., & Ladd, P. G. Using population viability analysis to predict the effect of fire on the extinction risk of an endangered shrub <i>Verticordia fimbriolepis</i> subsp. <i>fimbriolepis</i> in a fragmented landscape. <i>Plant Ecology</i> . 211(2) , 305-319. (2010).
<i>Caladenia argocalla</i>	Plantae	Displays senescence	0.664	Tremblay, R. L. <i>et al.</i> Population dynamics of <i>Caladenia</i> : Bayesian estimates of transition and extinction probabilities. <i>Australian Journal of Botany</i> . 57(4) , 351. (2009).
<i>Caladenia elegans</i>	Plantae	Displays senescence		Tremblay, R. L. <i>et al.</i> Population dynamics of <i>Caladenia</i> : Bayesian estimates of transition and

			0.820	extinction probabilities. <i>Australian Journal of Botany</i> . 57(4) , 351. (2009). <i>Journal of Botany</i> , 57(4), 351.
<i>Caladenia macroclavia</i>	Plantae	Displays senescence	0.652	Tremblay, R. L. <i>et al.</i> Population dynamics of <i>Caladenia</i> : Bayesian estimates of transition and extinction probabilities. <i>Australian Journal of Botany</i> . 57(4) , 351. (2009).
<i>Cirsium pitcher</i>	Plantae	Displays senescence	0.687	Halsey, S. J., Bell, T. J., McEachern, K., & Pavlovic, N. B. Population-specific life histories contribute to metapopulation viability. <i>Ecosphere</i> . 7(11), 15-36. (2016).
<i>Cyrtandra dentata</i>	Plantae	Displays senescence	0.824	Bialic-Murphy, L., Gaoue, O. G., & Kawelo, K. Microhabitat heterogeneity and a non-native avian frugivore drive the population dynamics of an island endemic shrub, <i>Cyrtandra dentata</i> . <i>Journal of Applied Ecology</i> . 54(5) , 1469-1477. (2017).
<i>Dendrophylax lindenii</i>	Plantae	Escapes senescence	1.051	Raventos J., Gonzalez, E., Mujica, E., & Doak, D. F. Population Viability Analysis of the Epiphytic Ghost Orchid (<i>Dendrophylax lindenii</i>) in Cuba. <i>Biotropica</i> . 47(2) , 179-189. (2015).
<i>Echinacea angustifolia</i>	Plantae	Escapes senescence	1.013	Dykstra, PhD thesis, 2013.
<i>Frasera speciose</i>	Plantae	Displays senescence	0.049	Che-Castaldo, J. P., & Inouye, D. W. The effects of dataset length and mast seeding on the demography of <i>Frasera speciosa</i> , a long-lived monocarpic plant. <i>Ecosphere</i> . 2(11) , 126. (2011).
<i>Lepanthes rubripetala</i>	Plantae	Escapes senescence	1.786	Schödelbauerová I., Tremblay, R. L., & Kindlmann, P. Prediction vs. reality: Can a PVA model predict population persistence 13 years later? <i>Biodiversity and Conservation</i> . 19(3) , 637-650. (2009).
<i>Vella pseudocytisus</i>	Plantae	Displays senescence		Lozano, F. D., Saiz, J. C. M., & Schwartz, M. W. Demographic

<i>pau</i>	modeling and monitoring cycle in a long-lived endangered shrub. <i>Journal for Nature Conservation</i> . 19(6) , 330-338. (2011).
0.916	

<i>Zamia inermis</i>	Plantae	Escapes senescence	1.820	Octavio-Aguilar, P. <i>et al.</i> Extinction risk of <i>Zamia inermis</i> : a demographic study in its single natural population. <i>Biodiversity and Conservation</i> . 26(4) , 787-800. (2017).
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442 **Supplementary Methods: ‘R’ computer code to extract age trajectories of fertility and**
 443 **mortality from population projection matrices, and to calculate Keyfitz’ entropy.**

444

445 #Code to quantify lx, mx and H, as calculated in:

446 #Senescence: Still an Unsolved Problem of Biology

447 #Mark Roper, Pol Capdevila & Roberto Salguero-Gómez

448 #Submitted to Nature.

449 #Code adapted by P.Capdevila (University of Oxford) and M.Roper (University of Oxford) from Jones et al.
 450 Diversity of ageing across the tree of life. *Nature*. 2014.

451 #Email: Mark Roper <mark.roper@keble.ox.ac.uk>

452 #Using equations from H. Caswell (2001) Matrix Population Models. 2nd Edition. #Sinauer, Sunderland, MA.
 453 Specific equations and pages within the references are #cited in each of the functions below.

454 #Last modified: June 18th, 2019

455 #Packages necessary:

456 require(MASS, popbio, popdemo)

457 ###Functions

458 #Function to trim down lx and mx at a given percentage before stationary convergence (See Methods).

459 qsdConvergence <- function(survMatrix, beginLife){

460 uDim <- dim(survMatrix)

461 eig <- eigen.analysis(survMatrix)

462 qsd <- eig\$stable.stage

463 qsd <- as.numeric(t(matrix(qsd / sum(qsd))))

464 #Set up a cohort

```
465     nzero <- rep(0, uDim[1]) #Set a population vector of zeros
466     nzero[beginLife] <- 1 #Set the first stage to =1
467     n <- nzero #Rename for convenience
468     #Iterate the cohort (n= cohort population vector, p = proportional structure)
469     dist <- p <- NULL
470     survMatrix1 <- survMatrix
471     for (j in 1:1500){ #j represent years of iteration
472         p <- n / sum(n) #Get the proportional distribution
473         dist[j] <- 0.5 * (sum(abs(p - qsd)))
474         n <- survMatrix1 %*% n #Multiply the u and n matrices to iterate
475     }
476     #Find the ages for convergence to 0.1, 0.05, and 0.01
477     pick1 <- min(which(dist < 0.1))
478     pick2 <- min(which(dist < 0.05))
479     pick3 <- min(which(dist < 0.01))
480     convage <- c(pick1, pick2, pick3)
481     return(convage)
482 }
483
484 #Function to determine probability of reaching reproduction, age at maturity and reproductive lifespan (Code
485 adapted from H. Caswell's matlab code):
486 lifeTimeRepEvents <- function(matU, matF, startLife = 1){
487     uDim <- dim(matU)[1]
488     surv <- colSums(matU)
489     repLifeStages <- colSums(matF)
490     repLifeStages[which(repLifeStages>0)] <- 1
491     if(missing(matF) | missing(matU)){stop('matU or matF missing')}
492     if(sum(matF,na.rm=T)==0){stop('matF contains only 0 values')}
493
494     #Age at first reproduction (La; Caswell 2001, p 124)
495     D <- diag(c(Bprime[2,]))
496     Uprimecond <- D%*%Uprime%*%ginv(D)
497     expTimeReprod <- colSums(ginv(diag(uDim)-Uprimecond))
498     out$La <- expTimeReprod[startLife]
499 }
500
```

```
501 #Function to create a life table
502 makeLifeTable<-function(matU, matF = NULL, matC = NULL, startLife = 1, nSteps = 1000){
503   matDim <- ncol(matU)
504   #Age-specific survivorship (lx) (See top function on page 120 in Caswell 2001):
505   matUtemp <- matU
506   survivorship <- array(NA, dim = c(nSteps, matDim))
507   for (o in 1:nSteps){
508     survivorship[o, ] <- colSums(matUtemp %**% matU)
509     matUtemp <- matUtemp %**% matU
510   }
511
512   lx <- survivorship[, startLife]
513   lx <- c(1, lx[1:(length(lx) - 1)])
514
515   #Start to assemble output object where we will store the data
516   out <- data.frame(x = 0:(length(lx)-1),lx = lx)
517
518   if(!missing(matF)){
519     if(sum(matF,na.rm=T)==0){
520       warning("matF contains only 0 values")
521     }
522   #Age-specific fertility (mx, Caswell 2001, p. 120)
523   ageFertility <- array(0, dim = c(nSteps, matDim))
524   fertMatrix <- array(0, dim = c(nSteps, matDim))
525   matUtemp2 <- matU
526   e <- matrix(rep(1, matDim))
527   for (q in 1:nSteps) {
528     fertMatrix <- matF %**% matUtemp2 * (as.numeric((ginv(diag(t(e) %**% matUtemp2))))))
529     ageFertility[q, ] <- colSums(fertMatrix)
530     matUtemp2 <- matUtemp2 %**% matU
531   }
532   mx <- ageFertility[, startLife]
533   mx <- c(0, mx[1:(length(mx) - 1)])
534   out$mx <- mx
535 }
536
```

```
537  ##Calculations from COMPADRE and COMADRE
538  #Upload COMPADRE and COMADRE
539  load("COMADRE_v.3.0.0.RData")
540  load("COMPADRE_v.5.0.0.RData")
541  indexPopCOMADRE=1:dim(comadre$metadata)[1]
542  indexPopCOMPADRE=1:dim(compadre$metadata)[1]
543  allPopIndex<- c(indexPopCOMADRE,indexPopCOMPADRE)
544  ###Loop to obtain demographic quantities
545  longPop<- dim(compadre$metadata)[1]
546  output<- data.frame("SpeciesAccepted"<- rep(NA,longPop),
547                    "MatrixDimension"<- rep(NA,longPop),
548
549                    "H"<- rep(NA,longPop),
550                    "La"<- rep(NA,longPop),
551                    "lx"<- rep(NA,longPop),
552                    "ux"<- rep(NA,longPop),
553                    "mx"<- rep(NA,longPop))
554
555  #Start the loop to make the calculations
556  for (i in 1:longPop){
557    index<- allPopIndex[i]
558    if (i<=length(indexPopCOMADRE)) {d=comadre} else {d=compadre}
559    #Define the name of the species
560    output[i,c("SpeciesAccepted")]<- unlist(lapply(d$metadata[index,c("SpeciesAccepted")], as.character))
561    #The calculations here employed define the beginning of life when an individual become established.
562    #Thus, we do not consider transitions from the "prop" stages
563    lifeStages<- d$matrixClass[[index]][1]
564    output[i,"stages"]=paste0(d$matrixClass[[index]][2])
565    notProp<- min(which(lifeStages != "prop"))
566    dorm<- which(lifeStages=="dorm")
567    matU<- d$mat[[index]]$matU
568    matU[is.na(matU)] <- 0
569    matF<- d$mat[[index]]$matF
570    matF[is.na(matF)] <- 0
571    matC<- d$mat[[index]]$matC
572    matC[is.na(matC)] <- 0
```

```
573   matA<- matU+matF+matC
574   #Store matrix dimension
575   output$MatrixDimension[i]=matDim=dim(matU)[1]
576   #Convergence to the quasi-stationary distribution
577   QSD <- qsdConvergence(matU,notProp)
578   #Calculate the life table
579   lifeTable <- makeLifeTable(matU,matF,matC,notProp,1000)[1:QSD[2],]
580   #Calculate and store Age at sexual maturity La
581   La <- output[i, "La"] <- lifeTimeRepEvents(matU,matF,notProp)
582   #Survival curve
583   output[i,"lx"][[1]] <- list(unlist(lifeTable$lx[1:QSD[2]]))
584   #Survival with the beginning of lx set at age at maturity
585   output[i,"lxs"][[1]] <- list(unlist(lifeTable$lx)[La:QSD[2]])
586   #Fertility curve
587   output[i,"mx"][[1]] <- list(unlist(lifeTable$mx)[1:QSD[2]])
588   #Fertility curve setting the beginning at age at maturity
589   output[i,"mxs"][[1]] <- list(unlist(lifeTable$mx)[La:QSD[2]])
590   #Define age
591   output[i,"x"][[1]] <- list(unlist(lifeTable$x)[1:QSD[2]])
592   #Define age since starting at age at maturity
593   output[i,"xs"][[1]] <- list(unlist(lifeTable$x)[La:QSD[2]])
594   #Keyfitz' entropy estimation
595   output$H[i] <- as.numeric(-
596   t(lx[is.na(lx)==FALSE])%*%log(lx[is.na(lx)==FALSE])/sum(lx[is.na(lx)==FALSE]))
597   }
598
```

599 **Source data**

600 COMADRE_v.3.0.0 (as file)

601 COMPADRE_v.5.0.0 (as file)

602