Senescence: Still an Unsolved Problem of Biology

Mark Roper*, Pol Capdevila & Roberto Salguero-Gómez

Abstract

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

Main

The evolution of senescence has long been explained by a collation of theories defining the 'classical evolutionary framework of ageing'. The central logic common to the theories argues that the force of natural selection weakens with age[1,4,5,6]. Selection becomes too weak to oppose the accumulation of genes that negatively affect older age classes[1], or favours these genes if they also have beneficial effects at earlier ages in life[5], when the contribution individuals make to future populations is assumed to be greater. Selection, therefore, should favour resource investment into earlier reproduction rather than late-life maintenance[6]. Ultimately, these theories predict, directly[4] or indirectly[1,5], that senescence is inescapable[4], or at least inevitable in organisms with clear germline-soma separation[5,6].

It takes one example to disprove any rule. Recently, a comparative description of demographic patterns of ageing in 46 species of animals, plants, and algae[8] contradicted the predictions of the classical evolutionary framework. Many of the examined species displayed negligible[10] or even negative[11] senescence, where the risk of mortality remains constant or decreases with age, and reproduction remains constant or increases with age. This mismatch between observations and expectations have rendered the classical evolutionary framework insufficient to explain the evolution of senescence across the tree of life. We now need to understand mechanisms behind such variation of ageing patterns[9], and how prevalent such "exceptions" are to the rule of ageing.

Here, we utilise high-resolution demographic information for 48 animal[2] and 260 plant[3] species worldwide to (i) provide a quantitative evaluation of the rates of actuarial senescence – the progressive age-dependent increase in mortality risk with age after maturation – across multicellular organisms, (ii) test whether the classical evolutionary framework explains the examined diversity of senescence rates, with special attention to predictions from germ-soma separation, and (iii) propose how to widen the classical evolutionary framework of ageing to better encompass the tree of life.

First, we derived life tables[12] from a selection of species' matrix population models[13], each of which are a summary of the population dynamics of the species in question under natural conditions (See Methods & Supplementary Information). We then quantified the rate of actuarial senescence on the survivorship trajectory of each species' life table using Keyfitz' entropy (H)[14]. This metric quantifies the spread and timing of mortality events in a cohort as individuals age, with H <1 indicating that most mortality occurs later in life (*i.e.* actuarial senescence), and H>1 indicating low mortality at advanced ages, whereby individuals may escape actuarial senescence (See Methods & Supplementary Information). Importantly, H is normalised by mean life expectancy, facilitating cross-species comparison to examine general patterns and plausible mechanisms.

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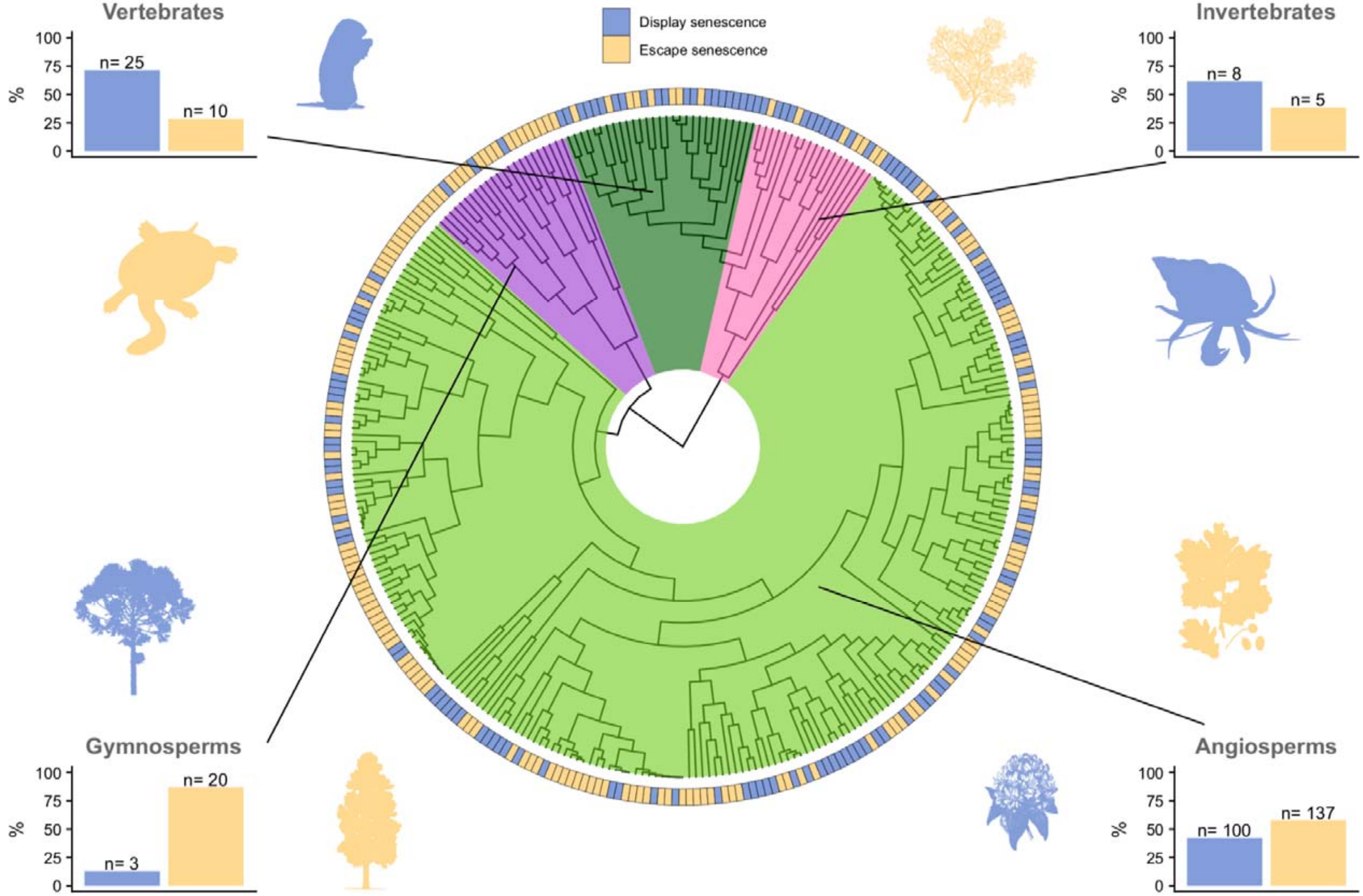

Vertebrates
Invertebrates
Gymnosperms
Angiosperms
Display senescence
Escape senescence
%
100
75
50
25
0
n= 25
n= 10
n= 8
n= 5
n= 3
n= 20
n= 100
n= 137

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

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

The central assumption of the classical evolutionary framework of ageing, that the force of natural selection weakens with age, rests on the assumption that older individuals contribute less to future populations[1,4,5,6]. This is both because fewer individuals survive to later age classes[1], and individuals are expected to favour reproduction at young rather than old ages[1,5,6]. To observe how different age classes contribute to future populations in our study species, we use the derived life tables[12] to quantify age-specific reproduction rates (*m(x)*) for species that we previously identified to display actuarial senescence (H<1) *vs.* those that do not (H>1) (See Methods & Supplementary information). The *m(x)* trajectories for all the species in our dataset can be found in Extended Data Fig. 1. For practicality, here, we provide the trajectories for the eight representative species across the four clades depicted in Figure 1.

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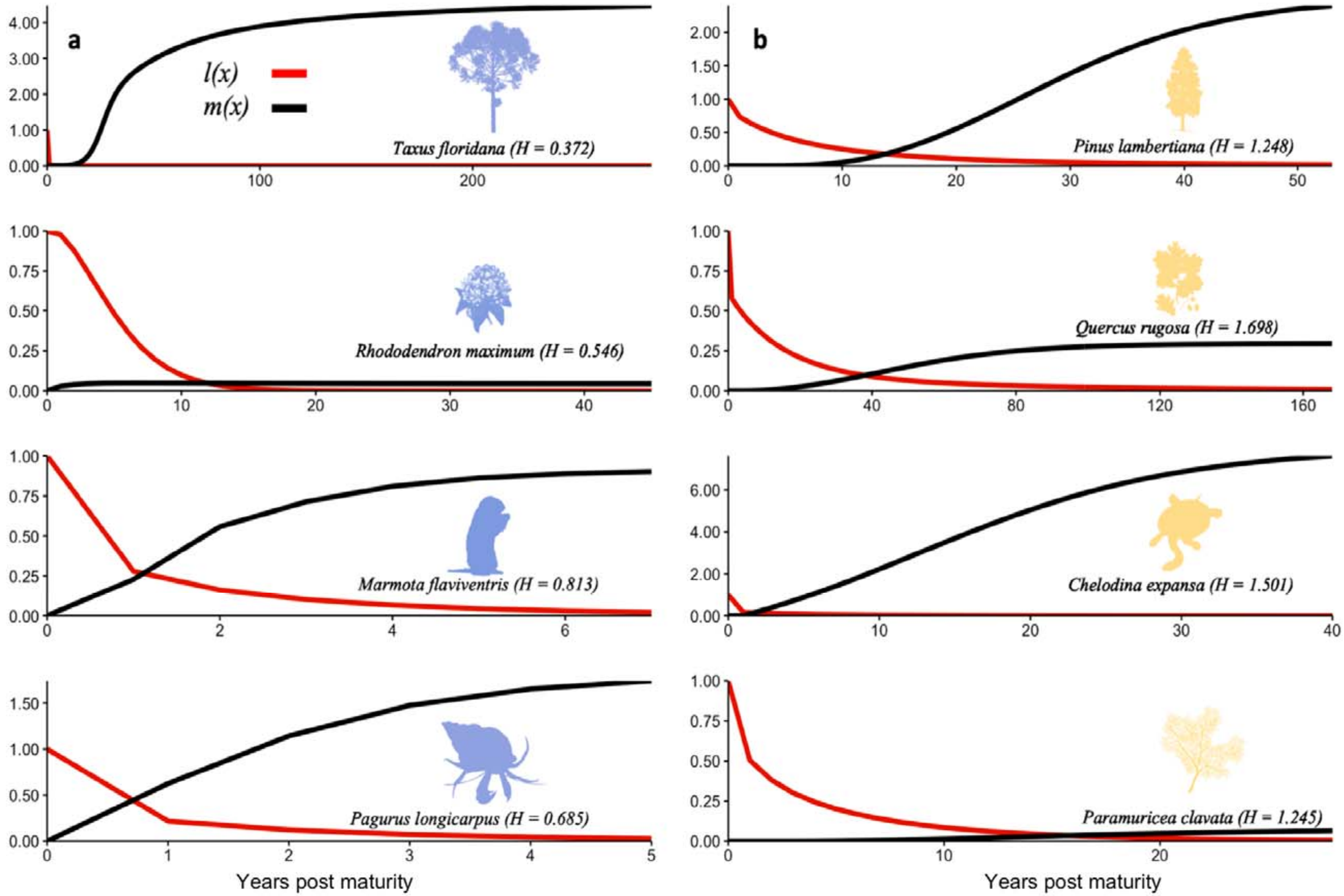

a
l(x)
m(x)
Taxus floridana (H = 0.372)
b
Pinus lambertiana (H = 1.248)
Rhododendron maximum (H = 0.546)
Quercus rugosa (H = 1.698)
Marmota flaviventris (H = 0.813)
Chelodina expansa (H = 1.501)
Pagurus longicarpus (H = 0.685)
Paramuricea clavata (H = 1.245)
Years post maturity
Years post maturity

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

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

Studies on reproductive senescence are sparser than their actuarial senescence counterparts. Although, important longitudinal investigations into reproductive senescence have been conducted[16,17,18], and current data suggest that rates of reproduction, like mortality hazards, can also both increase or decrease with age. Our results support observations that patterns of reproduction are variable across species (Fig. 2, Extended Data Fig. 1). Developing a methodology to quantify these senescence patterns of reproduction, as done here using Keyfitz' entropy[14] (*H*) for actuarial senescence, should be a focus of future theoretical work to unearth when, where, and what mechanisms drive how tightly the two components of senescence co-vary.

In general, our results display the discrepancy between the predictions of the classical evolutionary framework of ageing and empirical data. We suggest that researchers must widen the framework to better encompass the biology of a more diverse range of taxa. For example, the models of the classical evolutionary framework are purely age-structured, yet, in some species, demographic patterns of survival and reproduction may be influenced equally or even more by factors besides age[13]. Indeed, the force of selection does not always decline with age for some species[19]. These organisms display demographic trajectories of survival and reproduction that are better predicted by size rather than age, such as many plants[20], which is supported by the 58% of studied plant species here that escape senescence, or corals[21] (e.g. *Paramuricea clavata;* Fig. 1).

Many of the predictions made explicit from the classical framework of ageing have, until recently, long stood the test of time. Higher rates of extrinsic mortality, *i.e*. deaths due to the background environment, are expected to accelerate rates of senescence, whereas juvenile mortality is predicted not to play a role in the evolution of senescence[5]. Theoretical advancements, however, have shown that to have a significant effect, extrinsic mortality must be age-dependent[22]. Also, by biasing the stable age distribution of a population towards younger ages, high birth rate can also reduce the strength of selection with age[23]. The strength of selection at a given age is dependent on both the abundance of individuals in a given age class *and* the respective reproductive value of that age class[4,23]. Following this logic, some species that display senescence yet retain high reproduction at old ages (e.g. *Marmota flaviventris* or *Pagurus longicarpus*; Fig. 1, Fig. 2) may have a stable age distribution biased towards younger individuals. This outcome would render selection too weak to promote an escape from senescence. Ultimately, how the environment shapes patterns of birth and deaths will dictate both the reproductive value of age classes and the stable age-distribution of the classes. In turn, the resulting dynamics of these pressures will affect the relative strengths of age-specific selection gradients[24] for mortality and reproduction, and therefore patterns of senescence.

Finally, we have only considered patterns of survival and reproduction with respect to effects on the focal individual. If an individual's survival and/or reproduction affects the fitness of others, however, and the interacting individuals are relatives, selection on the demographic age trajectories will also be weighted by these effects[25]. In our study, for example, the killer whale (*Orcinus orca*) experiences negligible actuarial senescence (H = 0.999) (Extended Data Fig. 1a). Killer whales are an exemplar where post-reproductive survival is hypothesised to have evolved due to the positive effects individuals can have on the survival and reproduction of offspring, *i.e.* 'grandmother hypothesis'[4,5,26]. This is consistent with our results. Further evidence is also beginning to accrue elsewhere that sociality may have an important role in driving patterns of senescence beyond the remits of 'grandmothering'[27.28].

The emerging picture of senescence across multicellular organisms is at odds with the widely cited predictions of the classical evolutionary framework[1,4,5,6]. What drives the evolution of senescence has attracted the attention of a vast research community, but we propose that the field would benefit immensely if the attention is shifted towards the underlying mechanisms allowing species to escape from senescence. We expect the greatest progress to be made by researchers honing their focus to widening the classic evolutionary theories to a framework not solely focused on age, but instead inclusive of the aforementioned factors and with a special focus on actuarial and reproductive senescence as potentially differing trajectories. Most ageing research likely stems from human desire to increase human health and life span[29]. This desire requires understanding the variation in patterns of senescence across the tree of life. For now, senescence remains an unsolved problem of biology.

Methods

Data

We used the COMADRE Animal Matrix Database[2] (v. 3.0.0) and COMPADRE Plant Matrix Database[3] (v. 5.0.0) to obtain age trajectories of survival and reproduction. These open-access data repositories consist of matrix population models[13] (MPMs) incorporating high-resolution demographic information on the survival and reproduction patterns of over 1,000 animal and plant species worldwide[2,3]. Both databases include information on species for which the data have been digitised and thoroughly error-checked. In addition, we contacted authors for clarifications when any doubt about the interpretation of the life cycle of the species emerged. We imposed a series of selection criteria to restrict our analyses to data of the highest quality possible.

(i) MPMs were parameterised with field data from non-disturbed, unmanipulated populations (*i.e.* natural populations) to best describe the species' age trajectories.

(ii) MPMs had dimension ≥3 × 3 (i.e. rows × columns). Generally, low dimensions MPMs lack quality for the estimation of life history traits[30]. This selection criterion also helps avoid problems with quick convergence to stationary equilibrium, at which point the estimates of life history trait values and rates of senescence become unreliable[8,31].

(iii) MPMs were only used when the entire life cycle was explicitly modelled including recordings of survival, development, and reproduction for all life cycle stages.

(iv) When MPMs existed for multiple populations within a given species, we calculated the arithmetic element-by-element mean MPM to obtain a single MPM per species.

(v) When multiple studies existed for the same species, we considered only the study of greater duration to ensure the highest temporal variation in the population dynamics was captured.

(vi) Studies of annual plant species modelled using seasonal projection matrices were not included; we chose only species using an annual time step. This is due to the difficulties of converting their population dynamics to an annual basis to compare with all other species' models.

(vii) Included MPMs have stage-specific survival values ≤ 1. In a small number of published models, the stage-specific survival values can exceed 1 due to clonality being hidden in the matrix, rounding errors, or other mistakes in the original model[2,3].

(viii) MPMs were from species of which phylogenetic data was available, to ensure we were able to account for phylogenetic relatedness on our models.

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

Displaying *vs* escaping senescence

MPMs are a summary of the population dynamics of a given species, from which we can calculate several life history traits. To do so, we first must decompose an MPM (***A)*** into its sub-components[13]:

U **–** containing the stage-specific survival rates

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

C – containing stage-specific per-capita clonality rates

$$\boldsymbol{A} = \boldsymbol{U} + \boldsymbol{F} + \boldsymbol{C} \qquad \text{equation 1}$$

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

$$l(x) = e^t U^x e^j \qquad x = 0, 1, \ldots \qquad \text{equation 2}$$

We considered survivorship trajectories beginning at the age of maturity (calculated following 5.47–5.54 in Caswell[13]) and ending at the age at which 5% survivorship from maturity occurs. This is because a cohort modelled by iteration of the ***U*** matrix eventually decays exponentially at a rate given by the dominant eigenvalue of ***U***, and converges to a quasi-stationary distribution given by the corresponding right eigenvector **w**. Once this convergence has happened, mortality remains constant with age, and so to prevent our conclusions being overly influenced by this assumption, we calculated the age at which the cohort had converged to within a specified percentage (5%) of the quasi-stationary distribution[8,31].

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

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

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

Phylogenetic analyses for actuarial senescence

After categorising species as displaying (*H*<1) or escaping (*H*>1) senescence, we accounted for the phylogenetic relatedness of the species studied to determine the influence of a species' evolutionary history in its likelihood of evolving or escaping senescence. To build the phylogenetic tree with the species included in this study, we used data from the Open Tree of Life[32] (OTL), a database that combines public available taxonomic and phylogenetic information across the tree of life. We first checked that the species names in our data were taxonomically accepted using the *taxize* R package[33]. Then, we obtained animal and plant phylogenetic trees form OTL for the list of species in our data using *rotl* R package[34]. The branch length of the resulting tree was computed using the *compute.brlen* function from the R package *ape*[35], with Grafen's[36] arbitrary branch lengths. Polytomies (*i.e.* >2 species with the same ancestor) were resolved using the function multi2di from *ape* package[35], which transforms polytomies into a series of random dichotomies with one or several branches of length zero.

To evaluate the role of phylogenetic relatedness in determining the patterns of variation of actuarial senescence we estimated Pagel's λ[15]. This metric is an index bounded between zero and one, where values ~0 indicate that the evolutionary history of the species explains little about the variation of the trait measured, and values ~1 suggest that that evolutionary history mostly explains the observed variation of the trait across the studied species. To estimate Pagel's λ we used the R package *motmot.2.0*[37]. A full summary of the phylogenetic signals obtained for each of the four monophyletic groups can be found in the Extended Data and Figures (Table 1).

Reproduction analysis

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

$$\mathbf{p}(x) = \frac{U^x e_j}{e^T U^x e_j} \quad x = 0,1,\ldots. \qquad \text{equation 4}$$

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

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

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

Code availability

Code used for analysis is available in the supplementary information.

Data availability

Data are available from the source data files in the supplementary information and from the COMPADRE Plant Matrix Database and COMADRE Animal Matrix Database (www.compadre-db.com).

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Acknowledgements

M.R was supported by funding from the Biotechnology and Biological Sciences Research Council (BBSRC) [grant number BB/M011224/1]. P.C. was supported by a Ramón Areces Foundation Postdoctoral Scholarship. This research emerged through funding by NERC R/142195-11-1 to R.S-G.

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Contributions

M.R. and R.S.G. conceived the project. M.R. and P.C conducted the analysis and produced all visualizations. M.R drafted the first version and together with P.C. and R.S.-G., revised and edited the manuscript.

Competing interests

The authors declare no competing interests.

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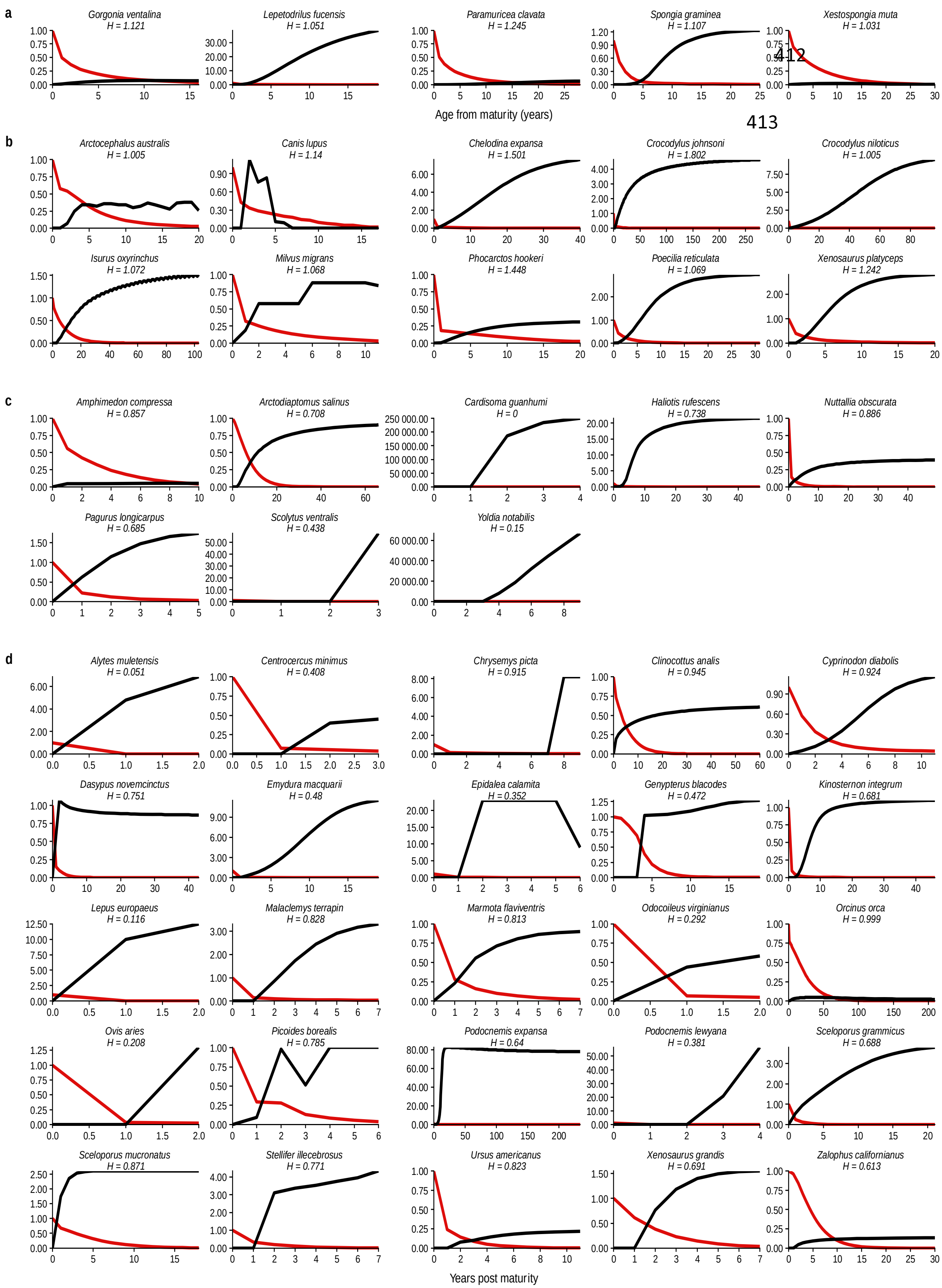
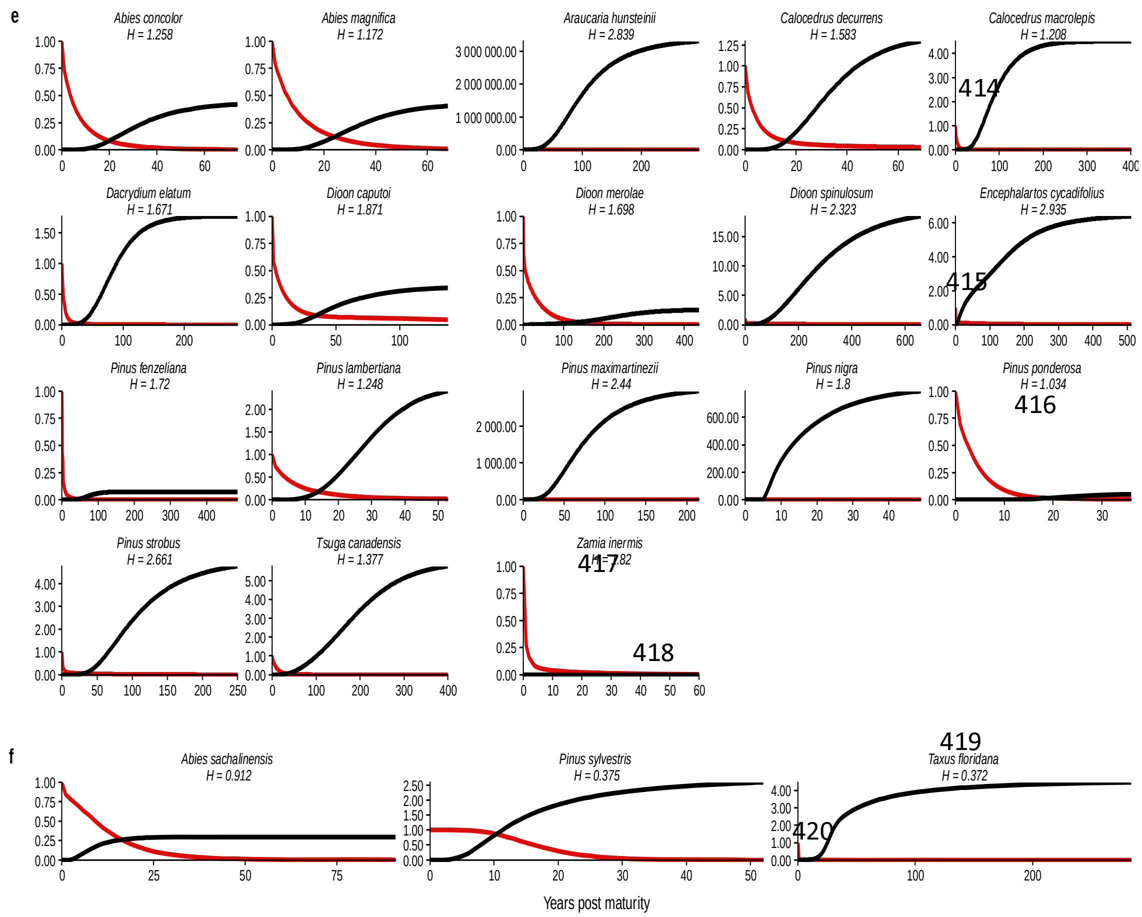
Extended data figures and tables

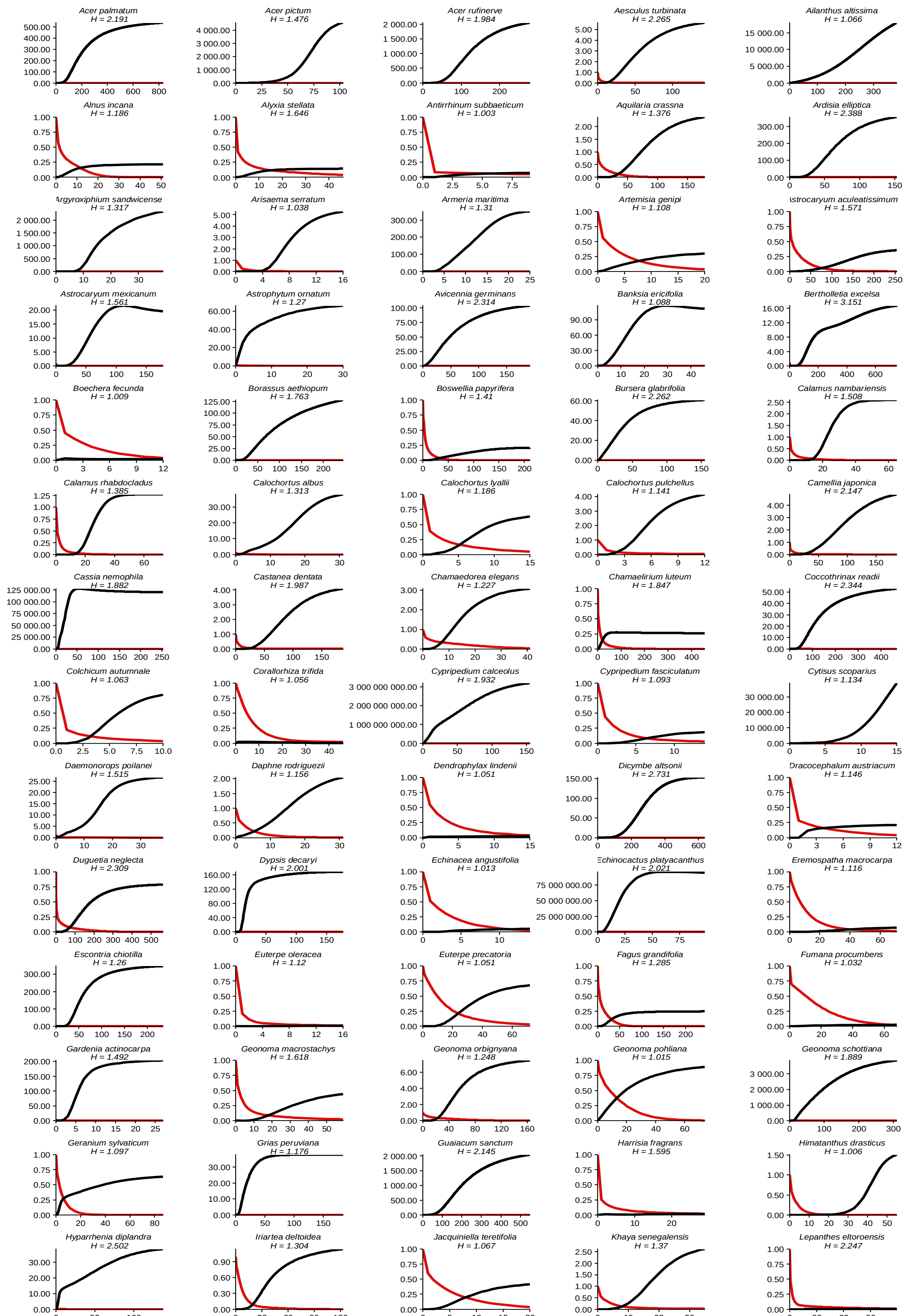
Fig. 1: Survivorship (red) and reproduction (black) age-trajectories for 306 of our study species. **a)** Invertebrates that escape senescence **b)** Vertebrates that escape senescence **c)** Invertebrates that display senescence **d)** Vertebrates that escape senescence **e)** Gymnosperms that escape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

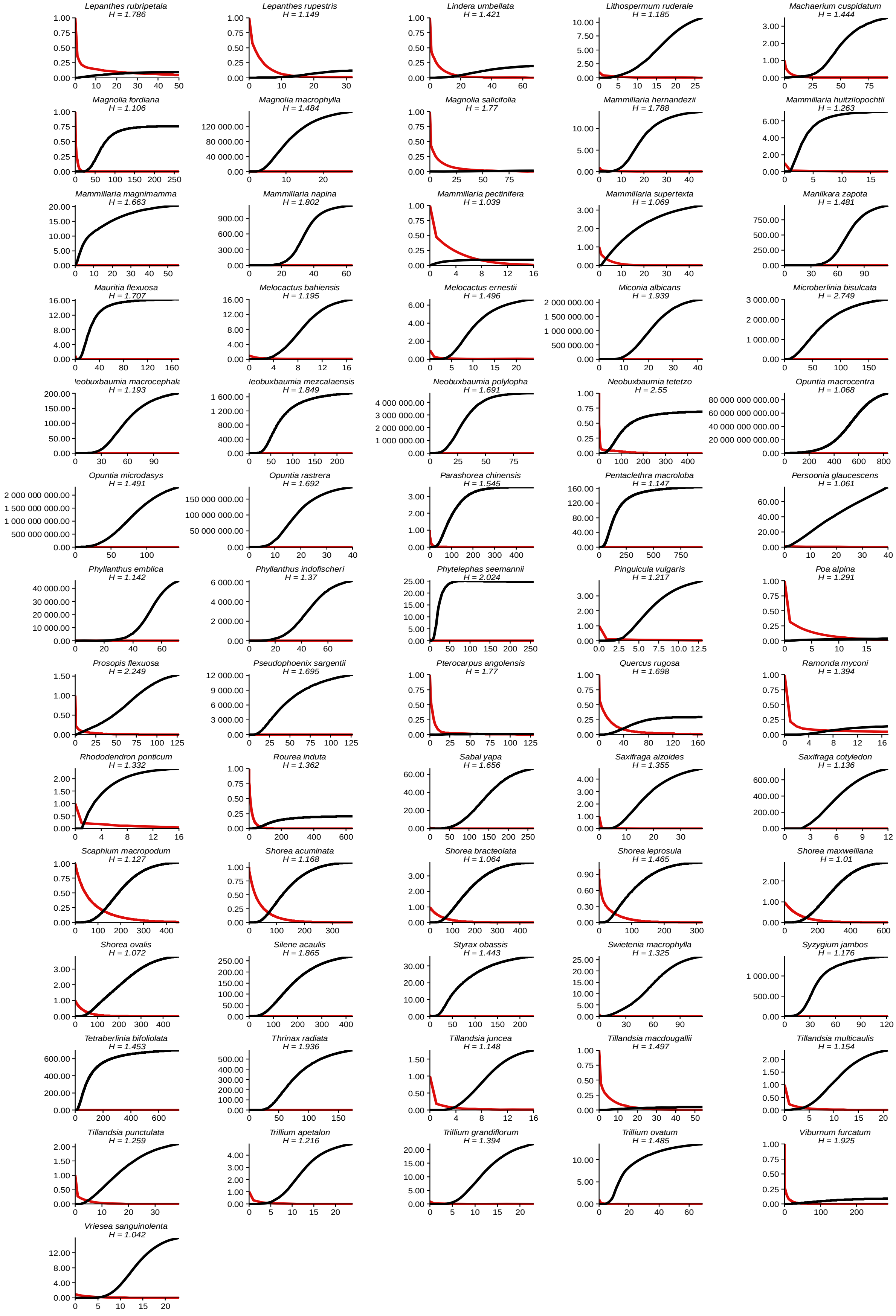

a
Gorgonia ventalina H = 1.121
Lepetodrilus fucensis H = 1.051
Paramuricea clavata H = 1.245
Spongia graminea H = 1.107
Xestospongia muta H = 1.031
Age from maturity (years)
b
Arctocephalus australis H = 1.005
Canis lupus H = 1.14
Chelodina expansa H = 1.501
Crocodylus johnsoni H = 1.802
Crocodylus niloticus H = 1.005
Isurus oxyrinchus H = 1.072
Milvus migrans H = 1.068
Phocarctos hookeri H = 1.448
Poecilia reticulata H = 1.069
Xenosaurus platyceps H = 1.242
c
Amphimedon compressa H = 0.857
Arctodiaptomus salinus H = 0.708
Cardisoma guanhumi H = 0
Haliotis rufescens H = 0.738
Nuttallia obscurata H = 0.886
Pagurus longicarpus H = 0.685
Scolytus ventralis H = 0.438
Yoldia notabilis H = 0.15
d
Alytes muletensis H = 0.051
Centrocercus minimus H = 0.408
Chrysemys picta H = 0.915
Clinocottus analis H = 0.945
Cyprinodon diabolis H = 0.924
Dasypus novemcinctus H = 0.751
Emydura macquarii H = 0.48
Epidalea calamita H = 0.352
Genypterus blacodes H = 0.472
Kinosternon integrum H = 0.681
Lepus europaeus H = 0.116
Malaclemys terrapin H = 0.828
Marmota flaviventris H = 0.813
Odocoileus virginianus H = 0.292
Orcinus orca H = 0.999
Ovis aries H = 0.208
Picoides borealis H = 0.785
Podocnemis expansa H = 0.64
Podocnemis lewyana H = 0.381
Sceloporus grammicus H = 0.688
Sceloporus mucronatus H = 0.871
Stellifer illecebrosus H = 0.771
Ursus americanus H = 0.823
Xenosaurus grandis H = 0.691
Zalophus californianus H = 0.613
Years post maturity

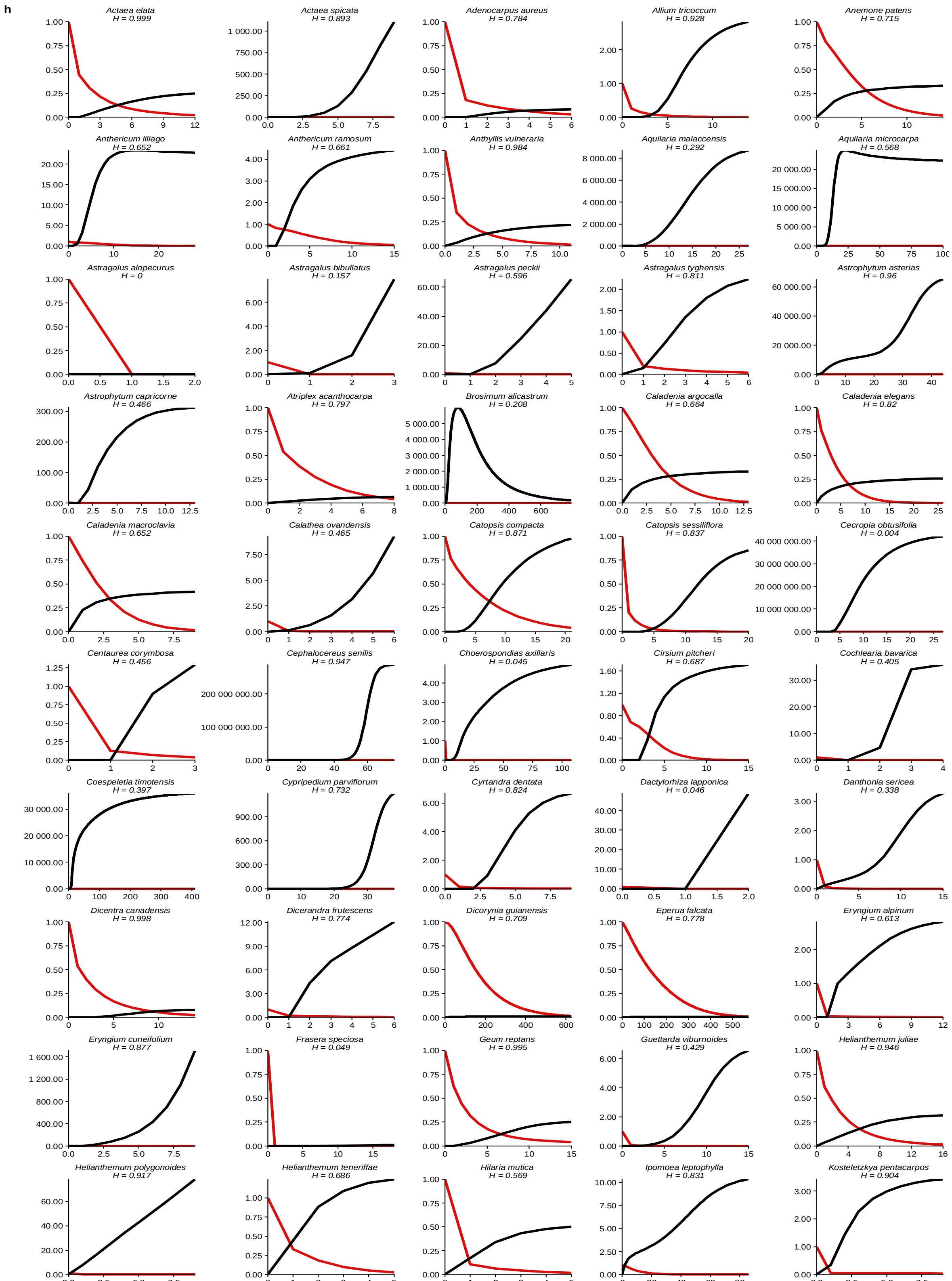

e
Abies concolor
H = 1.258
Abies magnifica
H = 1.172
Araucaria hunsteinii
H = 2.839
Calocedrus decurrens
H = 1.583
Calocedrus macrolepis
H = 1.208
Dacrydium elatum
H = 1.671
Dioon caputoi
H = 1.871
Dioon merolae
H = 1.698
Dioon spinulosum
H = 2.323
Encephalartos cycadifolius
H = 2.935
Pinus fenzeliana
H = 1.72
Pinus lambertiana
H = 1.248
Pinus maximartinezii
H = 2.44
Pinus nigra
H = 1.8
Pinus ponderosa
H = 1.034
Pinus strobus
H = 2.661
Tsuga canadensis
H = 1.377
Zamia inermis
f
Abies sachalinensis
H = 0.912
Pinus sylvestris
H = 0.375
Taxus floridana
H = 0.372
Years post maturity

422

g

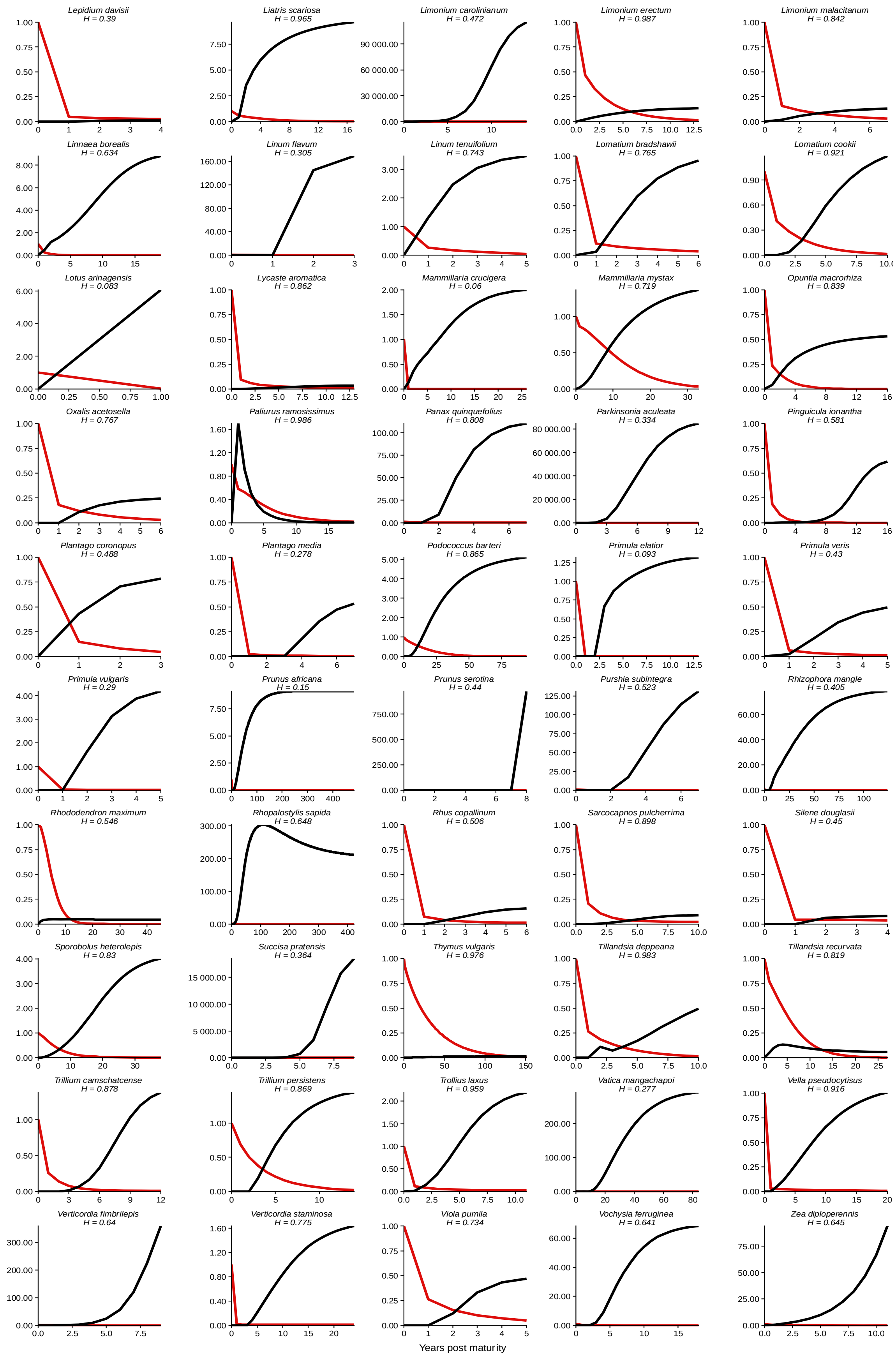



Lepanthes rubripetala H = 1.786
Lepanthes rupestris H = 1.149
Lindera umbellata H = 1.421
Lithospermum ruderale H = 1.185
Machaerium cuspidatum H = 1.444
Magnolia fordiana H = 1.106
Magnolia macrophylla H = 1.484
Magnolia salicifolia H = 1.77
Mammillaria hernandezii H = 1.788
Mammillaria huitzilopochtli H = 1.263
Mammillaria magnimamma H = 1.663
Mammillaria napina H = 1.802
Mammillaria pectinifera H = 1.039
Mammillaria supertexta H = 1.069
Manilkara zapota H = 1.481
Mauritia flexuosa H = 1.707
Melocactus bahiensis H = 1.195
Melocactus ernestii H = 1.496
Miconia albicans H = 1.939
Microberlinia bisulcata H = 2.749
Neobuxbaumia macrocephala H = 1.193
Neobuxbaumia mezcalaensis H = 1.849
Neobuxbaumia polylopha H = 1.691
Neobuxbaumia tetetzo H = 2.55
Opuntia macrocentra H = 1.068
Opuntia microdasys H = 1.491
Opuntia rastrera H = 1.692
Parashorea chinensis H = 1.545
Pentaclethra macroloba H = 1.147
Persoonia glaucescens H = 1.061
Phyllanthus emblica H = 1.142
Phyllanthus indofischeri H = 1.37
Phytelephas seemannii H = 2.024
Pinguicula vulgaris H = 1.217
Poa alpina H = 1.291
Prosopis flexuosa H = 2.249
Pseudophoenix sargentii H = 1.695
Pterocarpus angolensis H = 1.77
Quercus rugosa H = 1.698
Ramonda myconi H = 1.394
Rhododendron ponticum H = 1.332
Rourea induta H = 1.362
Sabal yapa H = 1.656
Saxifraga aizoides H = 1.355
Saxifraga cotyledon H = 1.136
Scaphium macropodum H = 1.127
Shorea acuminata H = 1.168
Shorea bracteolata H = 1.064
Shorea leprosula H = 1.465
Shorea maxwelliana H = 1.01
Shorea ovalis H = 1.072
Silene acaulis H = 1.865
Styrax obassis H = 1.443
Swietenia macrophylla H = 1.325
Syzygium jambos H = 1.176
Tetraberlinia bifoliolata H = 1.453
Thrinax radiata H = 1.936
Tillandsia juncea H = 1.148
Tillandsia macdougallii H = 1.497
Tillandsia multicaulis H = 1.154
Tillandsia punctulata H = 1.259
Trillium apetalon H = 1.216
Trillium grandiflorum H = 1.394
Trillium ovatum H = 1.485
Viburnum furcatum H = 1.925
Vriesea sanguinolenta H = 1.042
Years post maturity


h
Actaea elata H = 0.999
Actaea spicata H = 0.893
Adenocarpus aureus H = 0.784
Allium tricoccum H = 0.928
Anemone patens H = 0.715
Anthericum liliago H = 0.652
Anthericum ramosum H = 0.661
Anthyllis vulneraria H = 0.984
Aquilaria malaccensis H = 0.292
Aquilaria microcarpa H = 0.568
Astragalus alopecurus H = 0
Astragalus bibullatus H = 0.157
Astragalus peckii H = 0.596
Astragalus tyghensis H = 0.811
Astrophytum asterias H = 0.96
Astrophytum capricorne H = 0.466
Atriplex acanthocarpa H = 0.797
Brosimum alicastrum H = 0.208
Caladenia argocalla H = 0.664
Caladenia elegans H = 0.82
Caladenia macroclavia H = 0.652
Calathea ovandensis H = 0.465
Catopsis compacta H = 0.871
Catopsis sessiliflora H = 0.837
Cecropia obtusifolia H = 0.004
Centaurea corymbosa H = 0.456
Cephalocereus senilis H = 0.947
Choerospondias axillaris H = 0.045
Cirsium pitcheri H = 0.687
Cochlearia bavarica H = 0.405
Coespeletia timotensis H = 0.397
Cypripedium parviflorum H = 0.732
Cyrtandra dentata H = 0.824
Dactylorhiza lapponica H = 0.046
Danthonia sericea H = 0.338
Dicentra canadensis H = 0.998
Dicerandra frutescens H = 0.774
Dicorynia guianensis H = 0.709
Eperua falcata H = 0.778
Eryngium alpinum H = 0.613
Eryngium cuneifolium H = 0.877
Frasera speciosa H = 0.049
Geum reptans H = 0.995
Guettarda viburnoides H = 0.429
Helianthemum juliae H = 0.946
Helianthemum polygonoides H = 0.917
Helianthemum teneriffae H = 0.686
Hilaria mutica H = 0.569
Ipomoea leptophylla H = 0.831
Kosteletzkya pentacarpos H = 0.904

424

425


Lepidium davisii
H = 0.39
Liatris scariosa
H = 0.965
Limonium carolinianum
H = 0.472
Limonium erectum
H = 0.987
Limonium malacitanum
H = 0.842
Linnaea borealis
H = 0.634
Linum flavum
H = 0.305
Linum tenuifolium
H = 0.743
Lomatium bradshawii
H = 0.765
Lomatium cookii
H = 0.921
Lotus arinagensis
H = 0.083
Lycaste aromatica
H = 0.862
Mammillaria crucigera
H = 0.06
Mammillaria mystax
H = 0.719
Opuntia macrorhiza
H = 0.839
Oxalis acetosella
H = 0.767
Paliurus ramosissimus
H = 0.986
Panax quinquefolius
H = 0.808
Parkinsonia aculeata
H = 0.334
Pinguicula ionantha
H = 0.581
Plantago coronopus
H = 0.488
Plantago media
H = 0.278
Podococcus barteri
H = 0.865
Primula elatior
H = 0.093
Primula veris
H = 0.43
Primula vulgaris
H = 0.29
Prunus africana
H = 0.15
Prunus serotina
H = 0.44
Purshia subintegra
H = 0.523
Rhizophora mangle
H = 0.405
Rhododendron maximum
H = 0.546
Rhopalostylis sapida
H = 0.648
Rhus copallinum
H = 0.506
Sarcocapnos pulcherrima
H = 0.898
Silene douglasii
H = 0.45
Sporobolus heterolepis
H = 0.83
Succisa pratensis
H = 0.364
Thymus vulgaris
H = 0.976
Tillandsia deppeana
H = 0.983
Tillandsia recurvata
H = 0.819
Trillium camschatcense
H = 0.878
Trillium persistens
H = 0.869
Trollius laxus
H = 0.959
Vatica mangachapoi
H = 0.277
Vella pseudocytisus
H = 0.916
Verticordia fimbrilepis
H = 0.64
Verticordia staminosa
H = 0.775
Viola pumila
H = 0.734
Vochysia ferruginea
H = 0.641
Zea diploperennis
H = 0.645
Years post maturity

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

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

Supplementary information

Supplementary Table 1: Study species. Included species in our analysis were those that fitted the selection criteria described in methods. Species names, their kingdom (Animalia or Plantae), whether they display or escape actuarial senescence according to Keyfitz' entropy[14] (*H*), and the source study from which the data was originally compiled into COMADRE[2] and COMPADRE[3] are listed.

Species	Kingdom	Actuarial senescence	*H*	Source
Clinocottus analis	Animalia	Displays senescence	0.945	Davis, J., & Levin, L. Importance of pre-recruitment life-history stages to population dynamics of the woolly sculpin *Clinocottus analis*. *Marine Ecology Progress Series*. **234**, 229–246. (2002).
Cyprinodon diabolis	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. *PeerJ*. **2**, e549 (2014).
Genypterus blacodes	Animalia	Displays senescence	0.472	González-Olivares, E., Aránguiz-Acuña, A., Ramos-Jiliberto, R., & Rojas-Palma, A. Demographical analysis of the pink ling *Genypterus blacodes* (Schneider 1801) in the austral demersal fishery: A matrix approach evaluating harvest and non-harvest states. *Fisheries Research*, **96(2-3)**, 216–222. (2009).
Poecilia reticulata	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 (Poecilia reticulate). *Ecology*. **83(8**), 2194-2204. (2002).
Stellifer illecebrosus	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 *Stellifer illecebrosus* as a case study. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **22(5)**, 639–651. (2012).
Epidalea calamita	Animalia	Displays senescence		Di Minin, E., & Griffiths, R. A. Viability analysis of a threatened amphibian population: modelling

			0.352	the past, present and future. *Ecography*, **34(1),** 162–169. (2010).
Gorgonia ventalina	Animalia	Escapes senescence	1.121	Sabat, A.M., & Toledo-Hernandez, C. Viability of Sea Fan Populations Impacted by Disease: Recruitment versus Incidence. *Journal of Marine Biology*. Vol 2015, Article ID 987060. (2015).
Paramuricea clavata	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 *Paramuricea clavata*. *Marine Ecology Progress Series*, **402,** 59–68. (2010).
Centrocercus minimus	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. *Ecology and Evolution*, 4(22), 4247-4257 (2014).
Milvus migrans	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. *Basic and Applied Ecology*, **12(2),** 107–115. (2011).
Picoides borealis	Animalia	Displays senescence	0.785	Maguire, L. A., Wilhere, G. F., & Dong, Q. Population Viability Analysis for Red-Cockaded Woodpeckers in the Georgia Piedmont. *The Journal of Wildlife Management*, **59(3)**, 533. (1995).
Nuttallia obscurata	Animalia	Displays senescence	0.886	Dudas, S. E., Dower, J. F., & Anholt, B. R. Invasion dynamics of the varnish clam (*Nuttallia obscurata):* A matrix demographic modelling approach. *Ecology*, **88(8),** 2084–2093. (2007).
Yoldia notabilis	Animalia	Displays senescence	0.150	Nakaoka, M. Demography of the Marine Bivalve *Yoldia notabilis* in Fluctuating Environments: An Analysis Using a Stochastic Matrix Model. *Oikos*, **79(1)**, 59.

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

			0.438	1971.*The Canadian Entomologist*, **105(11),** 1465–1488. (1973)
Cardisoma guanhumi	Animalia	Displays senescence	0.000	Rodriguez-Fourquet, PhD thesis, 2004.
Pagurus longicarpus	Animalia	Displays senescence	0.685	Damiani, C. C. (2005). Integrating direct effects and trait-mediated indirect effects using a projection matrix model. *Ecology*, **86(8),** 2068–2074. (2005).
Canis lupus familiaris	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. *Urban Ecosystems*, **19(3),** 1405–1418. (2016).
Lepus europaeus	Animalia	Displays senescence	0.116	Marboutin, E., & Peroux, R. Survival Pattern of European Hare in a Decreasing Population. *The Journal of Applied Ecology*, **32(4**), 809. (1995).
Marmota flaviventris	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. *Am. Nat.* **173(4),** 517–530. (2009).
Odocoileus virginianus	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. *The Journal of Wildlife Management*, **79(2),** 211–219. (2015).
Orcinus orca	Animalia	Displays senescence	0.998	Velez-Espino, L.A. et al. Comparative demography and viability of northeastern Pacific resident killer whale populations at risk. *Can Tech Report Fish & Aq Sci.* (2014).
Ovis aries	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. *The Journal of Animal Ecology*, **61(2),** 381. (1992).
Phocarctos hookeri	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	*Phocarctos hookeri*. *Marine Biology*, **162(8),** 1587–1596. (2015).
Ursus americanus	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. *Ecological Modelling*, **294,** 51–58. (2014).
Zalophus californianus	Animalia	Displays senescence	0.612	Wielgus, J., Gonzalez-Suarez, M., Aurioles-Gamboa, D., & Gerber, L. R. A noninvasive demographic assessment of sea lions base don stage-specific abundances. *Ecological Applications,* **18(5),** 1287–1296. (2008).
Arctodiaptomus salinus	Animalia	Displays senescence	0.708	Jiménez-Melero, R., Gilbert, J., & Guerrero, F. Secondary production of *Arctodiaptomus salinus* in a shallow saline pond: comparison of methods. *Marine Ecology Progress Series*, **483**, 103–116. (2013).
Chelodina expansa	Animalia	Escapes senescence	1.501	Spencer, R.J., & Thompson, M.B. Experimental Analysis of the Impact of Foxes on Freshwater Turtle Populations. *Conservation Biology*, **19(3),** 845–854. (2005).
Chrysemys picta	Animalia	Displays senescence	0.915	Mitchell, J. C. Population Ecology and Life Histories of the Freshwater Turtles *Chrysemys picta* and *Sternotherus odoratus* in an Urban Lake. *Herpetological Monographs*, **2**, 40. (1988).
Crocodylus johnsoni	Animalia	Escapes senescence	1.802	Tucker, PhD Thesis, 1997. Smith, A.M.A & Webb, G.J.W. *Crocodylus johnstoni* in the McKinlay Area, N.T. VIII. A Population Simulation Model: *Wildlife Research* **12,** 541-554. (1985)
Crocodylus niloticus	Animalia	Escapes senescence	1.005	Hutton, PhD thesis, 1984.
Emydura macquarii	Animalia	Displays senescence	0.480	SPENCER, R.-J., & THOMPSON, M. B. (2005). Experimental Analysis of the Spencer, R.J., & Thompson, M.B. Experimental Analysis of the Impact of Foxes on Freshwater Turtle Populations. *Conservation Biology*, **19(3),** 845–854. (2005).
Kinosternon	Animalia	Displays senescence		Macip-Rios, R. et al.

integrum			0.681	Demography of two populations of the Mexican mud turtle (*Kinosternon integrum)* in central Mexico. *Herp J*. **21(4),** 235-245. (2011).
Malaclemys terrapin	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. *Journal of Applied Ecology*, *51(2),* 359–366. (2014).
Podocnemis lewyana	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 (*Podocnemis lewyana*): Implications for Management. *Copeia*, **103(4),** 1058–1074. (2015).
Podocnemis expansa	Animalia	Displays senescence	0.640	Mogollones, S. C., Rodríguez, D. J., Hernández, O., & Barreto, G. R. A Demographic Study of the Arrau Turtle (*Podocnemis expansa*) in the Middle Orinoco River, Venezuela. *Chelonian Conservation and Biology*, **9(1),** 79–89. (2010).
Sceloporus grammicus	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 *Sceloporus grammicus*. *Herpetologica*, **69(4),** 411–435. (2013).
Sceloporus mucronatus	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 *Sceloporus mucronatus. West N Am Naturalist.* **67(4),** 492-502. (2007).
Xenosaurus grandis	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 (*Xenosaurus grandis*) through the use of projection matrices. Copeia. 2, 324-335. (2007).
Xenosaurus platyceps	Animalia	Escapes senescence	1.242	Jones, C., Rojas-González, I., Lemos-Espinal, J., & Zúñiga-Vega, J. Demography of *Xenosaurus platyceps* (Squamata: Xenosauridae): a comparison between tropical and temperate populations. *Amphibia-Reptilia*, **29(2)**, 245–256. (2008).
Alytes muletensis	Animalia	Displays senescence	0.051	Pinya, S., Tavecchia, G. & Perez-Mellado, V. Population model of an endangered amphibian: implications for conservation management. *Endangered Species Research*. **34,** 123-130. (2017).
Arctocephalus australis	Animalia	Escapes senescence	1.004	Lima, M. & Paez, E. Demogrpahy and Population Dynamics of South American Fur Seals. *Journal of Mammalogy*. **78(3),** 914-920. (1997).
Dasypus novemcinctus	Animalia	Displays senescence	0.751	Oli, M.K. *et al.* Dynamics of leprosy in nine-banded armadillos: Net reproductive number and effects on host population dynamics. *Ecological Modelling*. **350,** 100-108. (2017).
Aspasia principissa	Plantae	Escapes senescence	1.163	Zotz, G., & Schmidt, G. Population decline in the epiphytic orchid *Aspasia principissa*. *Biological Conservation*, **129(1),** 82–90. (2006).
Catopsis compacta	Plantae	Displays senescence	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 epiphyteCatopsis compacta: a multidisciplinary approach. *Ecology and Evolution*, **3(11),** 3935–3946. (2013).
Catopsis sessiliflora	Plantae	Displays senescence	0.837	Winkler, M., Hülber, K., & Hietz, P. Population dynamics of epiphytic bromeliads: Life strategies and the role of host branches. *Basic and Applied Ecology*, **8(2),** 183–196. (2007).
Jacquiniella teretifolia	Plantae	Escapes senescence		Winkler, M., Hülber, K., & Hietz, P. Population dynamics of

			1.067	epiphytic orchids in a metapopulation context. *Annals of Botany*, **104(5),** 995–1004. (2009).
Lepanthes eltoroensis	Plantae	Escapes senescence	2.247	Tremblay, R.L. & Ackerman, J.D. Gene flow and effective population size in *Lepanthes (Orchidaceae*): a case for genetic drift. *Biological Journal of the Linnean Society*, **72(1),** 47–62. (2001).
Lepanthes rubripetala	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? *Biodiversity and Conservation.* **19(3)**, 637-650. (2009).
Lycaste aromatica	Plantae	Displays senescence	0.862	Winkler, M., Hülber, K., & Hietz, P. Population dynamics of epiphytic orchids in a metapopulation context. *Annals of Botany*, **104(5),** 995–1004. (2009).
Tillandsia deppeana	Plantae	Displays senescence	0.983	Winkler, M., Hülber, K., & Hietz, P. Population dynamics of epiphytic bromeliads: Life strategies and the role of host branches. *Basic and Applied Ecology*, **8(2),** 183–196. (2007).
Tillandsia juncea	Plantae	Escapes senescence	1.142	Winkler, M., Hülber, K., & Hietz, P. Population dynamics of epiphytic bromeliads: Life strategies and the role of host branches. *Basic and Applied Ecology*, **8(2),** 183–196. (2007).
Tillandsia macdougallii	Plantae	Escapes senescence	1.500	Mondragon Chopparo D., & Ticktin, T. Demographic Effects of Harvesting Epiphytic Bromeliads and an Alternative Approach to Collection. *Conservation Biology*, **25(4),** 797–807. (2011).
Tillandsia multicaulis	Plantae	Escapes senescence	1.154	Winkler, M., Hülber, K., & Hietz, P. Population dynamics of epiphytic bromeliads: Life strategies and the role of host branches. *Basic and Applied Ecology*, **8(2),** 183–196. (2007).
Tillandsia punctulata	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. *Acta Oecologica*, **59,** 52–61. (2014).
Tillandsia recurvata	Plantae	Displays senescence	0.819	Valverde, T. & Rocio, B. Is there demographic asynchrony among local populations of *Tillandsia recurvata?:* Evidence of tis metapopulation functioning. *Bol. Soc. Bot. Mex*. **n.86** (2010).
Vriesea sanguinolenta	Plantae	Escapes senescence	1.042	Zotz, G. Differences in vital demographic rates in three populations of the epiphytic bromeliad, *Werauhia sanguinolenta*. *Acta Oecologica*, **28(3),** 306–312. (2005).
Actaea spicata	Plantae	Displays senescence	0.893	Fröborg, H., & Eriksson, O. Predispersal seed predation and population dynamics in the perennial understorey herb *Actaea spicata*. *Canadian Journal of Botany*, **81(11),** 1058–1069. (2003).
Adenocarpus aureus gibbsianus	Plantae	Displays senescence	0.784	Iriondo; Albert; Giménez; Lozano; Escudero (2009). Book.
Allium tricoccum	Plantae	Displays senescence	0.928	Nault, A., & Gagnon, D. Ramet Demography of *Allium Tricoccum*, A Spring Ephemeral, Perennial Forest Herb. *The Journal of Ecology*, **81(1),** 101. (1993).
Anemone patens	Plantae	Displays senescence	0.715	Williams, J.L. & Crone, E.E. The impact of invasive grasses on the population growth of *Aneone patens*, a long-lived native forb. *Ecology*. **87 (12)** 3200-3208 (2006).
Anthericum liliago	Plantae	Displays senescence	0.652	Cerná, L., & Münzbergová, Z. (2013). Comparative Population Dynamics of Two Closely Related Species Differing in Ploidy Level. *PLoS ONE*. **8(10),** e75563. (2013).
Anthericum ramosum	Plantae	Displays senescence	0.661	Cerná, L., & Münzbergová, Z. Comparative Population Dynamics of Two Closely Related Species Differing in Ploidy Level. *PLoS ONE*. **8(10),** e75563. (2013).
Anthyllis vulneraria alpicola	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? *Annals of Botany*. **103(7),** 1129–1143. (2009).
Antirrhinum subbaeticum	Plantae	Escapes senescence	1.003	Iriondo; Albert; Gimemez; Lozana; Escuerdo. 978-84-8014-746-0
Boechera fecunda	Plantae	Escapes senescence	1.009	Lesica, P., & Shelly, J. S. Effects of reproductive mode on demography and life history in *Arabis fecunda* (Brassicaceae). *American Journal of Botany*. **82(6),** 752–762. (1995).
Arisaema serratum	Plantae	Escapes senescence	1.034	Kinoshita, E. Sex Change and Population Dynamics in *Arisaema serratum*. *Plant Species Biology*. **2(1-2),** 15–28. (1987).
Armeria maritima	Plantae	Escapes senescence	1.310	Lefebvre, C., & Chandler-Mortimer, A. Demographic Characteristics of the Perennial Herb Armeria maritima on Zilc Lead Mine Wastes. *The Journal of Applied Ecology*. **21(1),** 255. (1984).
Artemisia genipi	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? *Annals of Botany*. **103(7),** 1129–1143. (2009).
Astragalus alopecurus	Plantae	Displays senescence	0.000	Nicole, PhD thesis, 2005
Astragalus peckii	Plantae	Displays senescence	0.596	Martin, E. F., & Meinke, R. J. Variation in the demographics of a rare central Oregon endemic, *Astragalus peckii* Piper (Fabaceae), with fluctuating levels of herbivory. *Population Ecology*. **54(3),** 381–390. (2012).
Astragalus tyghensis	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. *Ecology*. **84(6)**, 1464-1476. (2003).
Calathea ovandensis	Plantae	Displays senescence		Horvitz, C. C., & Schemske, D. W. Spatiotemporal Variation in Demographic Transitions of a Tropical Understory Herb: Projection Matrix Analysis.

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

			1.093	Populations. *Conservation Biology*. **27(5),** 968-978. (2013).
Cypripedium parviflorum	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. *Journal of Ecology*. **102(5),** 1318-1328. (2014).
Dactylorhiza lapponica	Plantae	Displays senescence	10.46	Sletvold, N., Øien, D.-I., & Moen, A. Long-term influence of mowing on population dynamics in the rare orchid *Dactylorhiza lapponica*: The importance of recruitment and seed production. *Biological Conservation*. **143(3),** 747–755. (2010).
Danthonia sericea	Plantae	Displays senescence	0.338	Moloney, K. A. Fine-Scale Spatial and Temporal Variation in the Demography of a Perennial Bunchgrass. *Ecology*. 69(5), 1588–1598. (1988).
Dicentra canadensis	Plantae	Displays senescence	0.998	Lin, C.-H., Miriti, M. N., & Goodell, K. (Demographic consequences of greater clonal than sexual reproduction in Dicentra canadensis. Ecology and *Evolution*. **6(12),** 3871–3883. (2016).
Dicerandra frutescens	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. *Biological Conservation*. **127(1),** 115–127. (2006).
Dracocephalum austriacum	Plantae	Escapes senescence	1.146	Andrello, PhD thesis, 2010.
Eryngium alpinum	Plantae	Escapes senescence	0.613	Andrello, M. *et al*. Effects of management regimes and extreme climatic events on plant population viability in Eryngium alpinum. *Biological Conservation*. **147(1),** 99–106. (2012).
Eryngium cuneifolium	Plantae	Displays senescence	0.877	Menges, E. S., & Quintana-Ascencio, P. F. Population viability with fire in *Eryngium cuneifolium:* deciphering a decade of demographic data. *Ecological Monographs*. 7**4(1**), 79–99. (2004).
Geranium sylvaticum	Plantae	Escapes senescence		Ramula, S., Toivonen, E., & Mutikainen, P. Demographic

			1.097	Consequences of Pollen Limitation and Inbreeding Depression in a Gynodioecious Herb. *International Journal of Plant Sciences.* **168(4),** 443–453. (2007).
Geum reptans	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 *Geum reptans. Journal of Ecology*. **94(4),** 869–879. (2006).
Helianthemum polygonoides	Plantae	Displays senescence	0.917	Iriondo; Albert; Gimemez; Lozana; Escuerdo 978-84-8014-746-0
Helianthemum teneriffae	Plantae	Displays senescence	0.686	Iriondo; Albert; Gimemez; Lozana; Escuerdo 978-84-8014-746-0
Hilaria mutica	Plantae	Displays senescence	0.569	Vega, E., & Montaña, C. Spatio-temporal variation in the demography of a bunch grass in a patchy semiarid environment. *Plant Ecology Formerly `Vegetatio'*. **175(1),** 107–120. (2004).
Hyparrhenia diplandra	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. *Ecology.* **82(6)**, 1720-1733. (2001).
Ipomoea leptophylla	Plantae	Displays senescence	0.831	Keeler, K. H. Survivorship and Recruitment in a Long-lived Prairie Perennial, *Ipomoea leptophylla* (Convolvulaceae). *American Midland Naturalist.* **126(1),** 44. (1991).
Kosteletzkya pentacarpos	Plantae	Displays senescence	0.904	Pino, J., Pico, F. X., & De Roa, E. Population dynamics of the rare plant *Kosteletzkya pentacarpos* (Malvaceae): a nine-year study. *Botanical Journal of the Linnean Society*. **153(4),** 455–462. (2007).
Lepanthes rupestris	Plantae	Escapes senescence	1.145	Tremblay, R. L., & Ackerman J. D. Gene flow and effective population size in *Lepanthes (Orchidaceae)*: a case for genetic drift. *Biological Journal of the Linnean Society*. **72(1),** 47–62. (2001).
Lepidium davisii	Plantae	Displays senescence	0.390	Bernatus, Report, 1995.
Liatris scariosa	Plantae	Displays senescence		Ellis, M. M. *et al.* Matrix population models from 20

			0.965	studies of perennial plant populations. *Ecology*. **93(4),** 951–951. (2012).
Limonium carolinianum	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 *Limonium carolinianum*. *Canadian Journal of Botany*. **80(8),** 841–851. (2002).
Limonium erectum	Plantae	Displays senescence	0.987	Iriondo; Albert; Gimemez; Lozana; Escuerdo 978-84-8014-746-0
Limonium malacitanum	Plantae	Displays senescence	0.842	Iriondo; Albert; Gimemez; Lozana; Escuerdo 978-84-8014-746-0
Linum flavum	Plantae	Displays senescence	0.305	Münzbergová, Z. Comparative demography of two co-occurring Linum species with different distribution patterns. *Plant Biology*. **15(6),** 963–970. (2013).
Linum tenuifolium	Plantae	Displays senescence	0.743	Münzbergová, Z. Comparative demography of two co-occurring Linum species with different distribution patterns. *Plant Biology*. **15(6),** 963–970. (2013).
Lithospermum ruderale	Plantae	Escapes senescence	1.185	Bricker, M., & Maron, J. Post dispersal seed predation limits the abundance of a long-lived perennial forb *(Lithospermum ruderale*). *Ecology*. **93(3),** 532–543. (2012).
Lomatium bradshawii	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. *Ecology*. **84(6)**, 1464-1476 (2003).
Lomatium cookii	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. *Ecology*. **84(6)**, 1464-1476 (2003).
Lotus arinagensis	Plantae	Displays senescence	0.083	Iriondo; Albert; Gimemez; Lozana; Escuerdo 978-84-8014-746-0
Oxalis acetosella	Plantae	Displays senescence	0.767	Berg, H. Population dynamics in *Oxalis acetosella*: the significance of sexual reproduction in a clonal, cleistogamous forest herb. *Ecography*. **25(2),** 233–243. (2002).
Panax	Plantae	Displays senescence		Charron, D., & Gagnon, D. The

quinquefolius			0.801	Demography of Northern Populations of *Panax Quinquefolium* (American Ginseng). *The Journal of Ecology*. **79(2),** 431. (1991).
Pinguicula ionantha	Plantae	Displays senescence	0.581	Kesler, H. C., Trusty, J. L., Hermann, S. M., & Guyer, C. Demographic responses of *Pinguicula ionantha* to prescribed fire: a regression-design LTRE approach. *Oecologia*. **156(3),** 545–557. (2008).
Pinguicula vulgaris	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 Pinguicula. *The Journal of Ecology*. **81(4),** 635. (1993).
Plantago coronopus	Plantae	Displays senescence	0.488	Villellas, J. *et al.* Plant performance in central and northern peripheral populations of the widespread *Plantago coronopus. Ecography*. **36(2)**, 136-145. (2012).
Plantago media	Plantae	Displays senescence	0.273	Eriksson, Å., & Eriksson, O. Population dynamics of the perennial *Plantago media* in semi-natural grasslands. *Journal of Vegetation Science*. **11(2),** 245–252. (2000).
Poa alpina	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? *Annals of Botany*. **103(7),** 1129–1143. (2009).
Primula elatior	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.*Ecology*. **89(12**), 3480–3489. (2008).
Primula veris	Plantae	Escapes senescence	0.430	Lethilia, K., Syrjanen, K., Leimu, R., Garcia, M. B., & Ehrlen, J. Habitat Change and Demography of Primula veris: Identification of Management Targets. *Conservation Biology*. **20(3),** 833–843. (2006).
Primula vulgaris	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. *Ecography*. **37(3),** 230–240. (2013).
Ramonda myconi	Plantae	Escapes senescence	1.394	Xavier Picó, F., & Riba, M. *Plant Ecology*. **161(1),** 1–13. (2002).
Sarcocapnos pulcherrima	Plantae	Displays senescence	0.898	Salinas, M. J., Suárez, V., & Blanca, G. Demographic structure of three species of *Sarcocapnos (Fumariaceae*) as a basis for their conservation. *Canadian Journal of Botany*. **80(4),** 360–369. (2002).
Saxifraga aizoides	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? *Annals of Botany*. **103(7),** 1129–1143. (2009).
Saxifraga cotyledon	Plantae	Escapes senescence	1.136	Dinnétz, P., & Nilsson, T. Population viability analysis of *Saxifraga cotyledon*, a perennial plant with semelparous rosettes. *Plant Ecology*. **159(1)**, 61–71. (2002).
Silene acaulis	Plantae	Escapes senescence	1.865	Morris, W. & Doak, D. Life history of the long-lived gynodioecious cushion plant *Silene acaulis* (Caryophyllaceae), inferred from size-based population projection matrices. *Am J Bot*. **85(6**): 784. (1998).
Silene douglasii oraria	Plantae	Displays senescence	0.500	Kephart, S. R., & Paladino, C. Demographic change and microhabitat Variability in a Grassland Endemic, *Silene Douglasii Var. oraria (Caryophyllaceae).* *American Journal of Botany*. **84(2),** 179–189. (1997).
Sporobolus heterolepis	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. *American Journal of Botany*. **95(6),** 672–680. (2008).

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

			0.645	**90(4),** 684–692. (2002).
Alyxia stellata	Plantae	Escapes senescence	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. *Environmental Conservation*. **42(1),** 20–30. (2014).
Machaerium cuspidatum	Plantae	Escapes senescence	1.444	Nabe-Nielsen, J. Demography of *Machaerium cuspidatum*, a shade-tolerant neotropical liana. *Journal of Tropical Ecology*. **20(5),** 505–516. (2004).
Astrocaryum aculeatissimum	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. *Biodiversity and Conservation*. **19(8),** 2389–2403. (2010).
Astrocaryum mexicanum	Plantae	Escapes senescence	1.561	Pinero, D., Martinez-Ramos, M., & Sarukhan, J. A Population Model of *Astrocaryum Mexicanum* and a Sensitivity Analysis of its Finite Rate of Increase. The *Journal of Ecology*. **72(3),** 977. (1984).
Borassus aethiopum	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. *Journal of Tropical Ecology*. **16(5),** 637–655. (2000).
Calamus nambariensis	Plantae	Escapes senescence	1.508	Binh, PhD thesis, 2009.
Calamus rhabdocladus	Plantae	Escapes senescence	1.385	Binh, PhD thesis, 2009.
Chamaedorea elegans	Plantae	Escapes senescence	1.227	Valverde, T., Hernandez-Apolinar, M., & Mendoza-Amarom, S. Effect of Leaf Harvesting on the Demography of the Tropical Palm *Chamaedorea elegansin* South-Eastern Mexico. *Journal of Sustainable Forestry*. **23(1),** 85–105. (2006).
Coccothrinax readii	Plantae	Escapes senescence		Olmsted, I., & Alvarez-Buylla, E. R. Sustainable Harvesting of Tropical Trees: Demography and Matrix Models of Two Palm Species in Mexico. *Ecological*

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

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

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

			1.881	cassia under grazing pressure. *Oecologia*. **60(2),** 227–233. (1983).
Cytisus scoparius	Plantae	Escapes senescence	1.334	Neubert, M. G., & Parker, I. M. Projecting Rates of Spread for Invasive Species. *Risk Analysis.* **24(4),** 817–831. (2004).
Daphne rodriguezii	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. *Oikos.* **121(6),** 835–847. (2011).
Fumana procumbens	Plantae	Escapes senescence	1.032	Bengtsson, K. *Fumana Procumbens* on Oland--Population Dynamics of a Disjunct Species at the Northern Limit of its Range. *The Journal of Ecology*. **81(4),** 745. (1993).
Helianthemum juliae	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 *Helianthemum juliae* (CISTACEAE) in relation to climate variability. *Biological Conservation*. **136(4),** 552–562. (2007).
Lindera umbellata	Plantae	Escapes senescence	1.421	Hara, M., Kanno, H., Hirabuki, Y., & Takehara, A. Population dynamics of four understorey shrub species in beech forest. *Journal of Vegetation Science.* **15(4),** 475–484. (2004).
Linnaea borealis	Plantae	Displays senescence	0.634	Eriksson, O. Population structure and dynamics of the clonal dwarf-shrub *Linnaea borealis*. *Journal of Vegetation Science*. **3(1),** 61–68. (1992).
Magnolia salicifolia	Plantae	Escapes senescence	1.770	Hara, M., Kanno, H., Hirabuki, Y., & Takehara, A. Population dynamics of four understorey shrub species in beech forest. *Journal of Vegetation Science.* **15(4),** 475–484. (2004).
Miconia albicans	Plantae	Escapes senescence	1.939	Hoffmann, W. A. Fire and population dynamics of four understorey shrub species in beech forest. *Ecology*. **80(4),** 1354–1369. (1999).
Paliurus ramosissimus	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, *Paliurus ramosissimus (Lour.) Poir.*, using a shoot-dynamics matrix model. Population *Ecology*. **56(2),** 275–288. (2013).
Persoonia glaucescens	Plantae	Escapes senescence	1.061	McKenna, PhD thesis, 2007.
Purshia subintegra	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. *Conservation Biology*. **20(1),** 218–228. (2006).
Rhododendron maximum	Plantae	Displays senescence	0.546	McGraw, J. B. Effects of age and size on life histories and population growth of *Rhododendron maximum* shoots. *American Journal of Botany.* **76(1),** 113–123. (1989).
Rhus copallinum	Plantae	Displays senescence	0.506	Thaxton, PhD thesis, 2003.
Rourea induta	Plantae	Escapes senescence	1.362	Hoffmann, W. A. Fire and population dynamics of four understorey shrub species in beech forest. *Ecology*. **80(4),** 1354–1369. (1999).
Verticordia staminosa	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 *Verticordia staminosa (Myrtaceae)* with a highly restricted distribution. *Australian Journal of Botany.* **55(3),** 194. (2007).
Viburnum furcatum	Plantae	Escapes senescence	1.925	Hara, M., Kanno, H., Hirabuki, Y., & Takehara, A. Population dynamics of four understorey shrub species in beech forest. *Journal of Vegetation Science.* **15(4),** 475–484. (2004).
Astrophytum asterias	Plantae	Displays senescence	0.960	Martinez-Avalos, PhD thesis, 2007.
Astrophytum capricorne	Plantae	Displays senescence	0.468	Bravo Espinoza, PhD thesis, 2011.
Astrophytum ornatum	Plantae	Escapes senescence	1.270	V Zepeda-Martínez, MC Mandujano, FJ Mandujano, JK Golubov. What can the demography of *Astrophytum ornatum* tell us of its endangered status? *Journal of arid*

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

				167–184. (2004).
Mammillaria mystax	Plantae	Displays senescence	0.719	Saldivar Sanches, Navarro Carbajal, Cact Suc Mex, 2012.
Mammillaria napina	Plantae	Escapes senescence	1.802	Rodriguez Ortega, PhD thesis, 2008.
Mammillaria pectinifera	Plantae	Escapes senescence	1.039	Valverde, P.L. & Zavala-Hurtado, J.A. Assessing the ecological status of *Mammillaria pectinifera* Weber (cactaceae), a rare and threatened species endemic of the Tehuacan-Cuitcatlan Region in Central Mexico. *Journal of Arid Environments.* **64(2)** 193-208 (2006).
Mammillaria supertexta	Plantae	Escapes senescence	1.069	Avendano Calco, MSc thesis, 2007.
Neobuxbaumia macrocephala	Plantae	Escapes senescence	1.193	Esparza-Olguin, L., Valverde, T. & Mandujano, M.C. Comparative demographic analysis of three *Neobuxbaumia* species (cactaceae) with differing degree of rarity. *Population Ecology.* **47(3)** 229-245 (2005).
Neobuxbaumia mezcalaensis	Plantae	Escapes senescence	1.849	Esparza-Olguin, L., Valverde, T. & Mandujano, M.C. Comparative demographic analysis of three *Neobuxbaumia* species (cactaceae) with differing degree of rarity. *Population Ecology.* **47(3)** 229-245 (2005).
Neobuxbaumia polylopha	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. *Acta Oecologica*. **71**, 52-60 (2016)
Neobuxbaumia tetetzo	Plantae	Escapes senescence	2.550	Esparza-Olguin, L., Valverde, T. & Mandujano, M.C. Comparative demographic analysis of three *Neobuxbaumia* species (cactaceae) with differing degree of rarity. *Population Ecology.* **47(3)** 229-245 (2005).
Opuntia macrocentra	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. *Population Ecology*. **49(2),** 141–153. (2007).

Opuntia macrorhiza	Plantae	Displays senescence	0.839	Haridas, C. V., Keeler, K. H., & Tenhumberg, B. Variation in the local population dynamics of the short-lived *Opuntia macrorhiza (Cactaceae)*. *Ecology*. **96(3),** 800–807. (2015).
Opuntia microdasys	Plantae	Escapes senescence	1.491	Carrillo Angeles, PhD thesis, 2011.
Opuntia rastrera	Plantae	Escapes senescence	1.692	Mandujano, M. C., Montan~a, C., Franco, M., Golubov, J., & Flores-Martínez, A. Integration of demographic anual variability in a clonal desert cactus.*Ecology*. **82(2),** 344–359. (2001).
Abies concolor	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. *Journal of Ecology*. **93(4)**, 737-747 (2005)
Abies magnifica	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. *Journal of Ecology*. **93(4)**, 737-747 (2005)
Abies sachalinensis	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. *Journal of Vegetation Science*. **10(6),** 843–850. (1999).
Acer palmatum	Plantae	Escapes senescence	2.191	Tanaka, H. *et al.* Comparative demography of three coexisting Acer species in gaps and under closed canopy. *Journal of Vegetation Science*. **19(1),** 127–138. (2008).
Acer pictum	Plantae	Escapes senescence	1.476	Tanaka, H. *et al.* Comparative demography of three coexisting Acer species in gaps and under closed canopy. *Journal of Vegetation Science*. **19(1),** 127–138. (2008).
Acer rufinerve	Plantae	Escapes senescence	1.984	Tanaka, H. *et al.* Comparative demography of three coexisting Acer species in gaps and under closed canopy. *Journal of Vegetation Science*. **19(1),** 127–138. (2008).
Aesculus turbinata	Plantae	Escapes senescence	2.265	Kaneko, Y., Takada, T. & Kawana, S. Population biology of *Aesculus turbinate:* A

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

				L., & Martinez-Ramos, M. Gap-dependence in mangrove life-history strategies: a consideration of the entire life cycle and patch dynamics. *Journal of Ecology*. **95(6**), 1222–1233. (2007).
Bertholletia excelsa	Plantae	Escapes senescence	3.151	Zuidema, P. A., & Boot, R. G. A. Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics. *Journal of Tropical Ecology*. **18(1),** 1–31. (2002).
Boswellia papyrifera	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. *Journal of Applied Ecology*. **49(1),** 164–173. (2011).
Brosimum alicastrum	Plantae	Displays senescence	0.201	Peters, PhD thesis, 1989.
Bursera glabrifolia	Plantae	Escapes senescence	2.262	Hernández-Apolinar, M., Valverde, T., & Purata, S. Demography of *Bursera glabrifolia*, a tropical tree used for folk woodcrafting in Southern Mexico: An evaluation of its management plan. *Forest Ecology and Management*. **223(1-3),** 139–151. (2006).
Calocedrus decurrens	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. *Journal of Ecology*. **93(4),** 737–747. (2005).
Calocedrus macrolepis	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. *Population Ecology*. **50(2),** 227–237. (2008).
Camellia japonica	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. *Plant Spp Biol.* **22(3),** 175-190. (2007)
Castanea dentata	Plantae	Escapes senescence	1.987	Davelos, A. L., & Jarosz, A. M. Demography of American chestnut populations: effects of a pathogen and a hyperparasite. *Journal of Ecology*. **92(4),** 675–685. (2004).
Cecropia obtusifolia	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. *Am.Nat.* **143(1)**, 155–191. (1994).
Choerospondias axillaris	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. *Ecology*. **90(3),** 688–698. (2009).
Dacrydium elatum	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. *Population Ecology*. **50(2),** 227–237. (2008).
Dicorynia guianensis	Plantae	Displays senescence	0.709	Picard, N., Ouédraogo, D., & Bar-Hen, A. Choosing classes for size projection matrix models. *Ecological Modelling.* **221(19),** 2270–2279. (2010).
Dicymbe altsonii	Plantae	Escapes senescence	2.731	Zagt;Boot PhD thesis, 1997.
Duguetia neglecta	Plantae	Escapes senescence	2.301	Zagt;Boot PhD thesis, 1997.
Eperua falcata	Plantae	Displays senescence	0.778	Chagneau, P., Mortier, F., & Picard, N. (2009). Designing permanent sample plots by using a spatially hierarchical matrix population model. *Journal of the Royal Statistical Society: Series C (Applied Statistics).* **58(3),** 345–367. (2009).
Fagus grandifolia	Plantae	Escapes senescence	1.285	Batista, W. B., Platt, W. J., & Macchiavelli, R. E. Demography of a Shade-Tolerant Tree (*Fagus grandifolia*) in a Hurricane-Disturbed Forest. *Ecology*. **79(1),** 38. (1998).
Grias peruviana	Plantae	Escapes senescence	1.176	Peters, *Ecol & Manag Non-timber Forest Resources*, 1995.
Guaiacum	Plantae	Escapes senescence	2.145	CITES, Plants Committee, 2008.

sanctum				
Guettarda viburnoides	Plantae	Displays senescence	0.429	Loayza, A. P., & Knight, T. Seed dispersal by pulp consumers, not "legitimate" seed dispersers, increases *Guettarda viburnoides* population growth. *Ecology.* **91(9),** 2684–2695. (2010).
Himatanthus drasticus	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 *Himatanthus drasticus* (Apocynaceae): Implications for sustainable management. *Forest Ecology and Management.* **354**, 177–184. (2015).
Juniperus procera	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 *Juniperus procera* in Ethiopia. *Forest Ecology and Management.* **216(1-3**), 317–330. (2005).
Khaya senegalensis	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. *Conservation Biology.* **24(2),** 605–614. (2010).
Magnolia macrophylla dealbata	Plantae	Escapes senescence	1.484	Sánchez-Velásquez, L. R., & Pineda-López, M. del R. Comparative demographic analysis in contrasting environments of Magnolia dealbata: an endangered species from Mexico. *Population Ecology*. **52(1),** 203–210. (2009).
Magnolia fordiana	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. *Population Ecology*. **50(2),** 227–237. (2008).
Microberlinia bisulcata	Plantae	Escapes senescence	2.749	Norghauer, J. M., & Newbery, D. M. Seed fate and seedling dynamics after masting in two African rain forest trees. *Ecological Monographs.* **81(3),** 443–469. (2011).

Parashorea chinensis	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. *Population Ecology*. **50(2),** 227–237. (2008).
Parkinsonia aculeata	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. *Australian Journal of Entomology*. **45(4),** 308–316. (2006).
Pentaclethra macroloba	Plantae	Escapes senescence	1.147	Hartshorn, PhD thesis, 1972.
Phyllanthus emblica	Plantae	Escapes senescence	1.142	Ellis, M. M. *et al.* Matrix population models from 20 studies of perennial plant populations. *Ecology*. **93(4**), 951–951. (2012).
Phyllanthus indofischeri	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. *Journal of Applied Ecology*. **49(4),** 774–784. (2012).
Pinus fenzeliana	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. *Population Ecology*. **50(2),** 227–237. (2008).
Pinus lambertiana	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. Journal of *Ecology*. **93(4**), 737–747. (2005).
Manilkara zapota	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 Manilkara zapota (Sapotaceae). *Journal of Tropical Ecology*. **25(2),** 135–146. (2009).

Pinus maximartinezii	Plantae	Escapes senescence	2.440	López-Mata, L. The impact of seed extraction on the population dynamics of *Pinus maximartinezii*. *Acta Oecologica*, **49**, 39–44. (2013).
Pinus nigra	Plantae	Escapes senescence	1.780	Buckley, Y. M. *et al.* Slowing down a pine invasion despite uncertainty in demography and dispersal. *Journal of Applied Ecology*. **42(6)**, 1020–1030. (2005).
Pinus ponderosa	Plantae	Escapes senescence	1.034	Buckley, Y. M. *et al.* Slowing down a pine invasion despite uncertainty in demography and dispersal. *Journal of Applied Ecology*. **42(6)**, 1020–1030. (2005).
Pinus strobus	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 *Pinus strobus*. *PLoS ONE*. **8(2**), e56953. (2013).
Pinus sylvestris	Plantae	Displays senescence	0.375	Usher, M. B. A Matrix Approach to the Management of Renewable Resources, with Special Reference to Selection Forests. *The Journal of Applied Ecology*. **3(2),** 355. (1966).
Prosopis flexuosa	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 Prosopis flexuosa with contrasting grazing regimes in the Central Monte Desert. *Forest Ecology and Management***.** **369,** 184–190. (2016).
Prunus africana	Plantae	Displays senescence	0.150	Stewart, PhD thesis, 2001.
Prunus serotina	Plantae	Displays senescence	0.440	Sebert-Cuvillier, E. *et al.* Local population dynamics of an invasive tree species with a complex life-history cycle: A stochastic matrix model. *Ecological Modelling*. **201(2),** 127–143. (2007).
Pterocarpus angolensis	Plantae	Escapes senescence	1.770	Desmet, P.G., Shackleton, C.M. & Robinson, E.R. The population dynamics and life-history attributes of a *Pterocarpus angolensis* population in the Northern Province, South Africa.

				South African *Journal of Botany*. **62(3**) 160-166. (1996).
Quercus rugosa	Plantae	Escapes senescence	1.698	Bonil; Valverde (unpublished).
Rhizophora mangle	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. *Journal of Ecology*. **95(6),** 1222–1233. (2007).
Rhododendron ponticum	Plantae	Escapes senescence	1.332	Salguero-Gomez, MSc thesis, 2004.
Scaphium macropodum	Plantae	Escapes senescence	1.127	Yamada, T. *et al*. Strong habitat preference of a tropical rain forest tree does not imply large differences in population dynamics across habitats. *Journal of Ecology*. **95(2),** 332–342. (2007).
Shorea acuminata	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. *Oecologia*. **172(3),** 713–724. (2012).
Shorea bracteolata	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. *Oecologia*. **172(3),** 713–724. (2012).
Shorea leprosula	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. *Oecologia*. **172(3),** 713–724. (2012).
Shorea maxwelliana	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. *Oecologia*. **172(3),** 713–724. (2012).
Shorea ovalis	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. *Oecologia*. **172(3),** 713–724. (2012).
Stryphnodendron microstachyum	Plantae	Escapes senescence	2.009	Hartshorn, PhD thesis, 1972.
Styrax obassis	Plantae	Escapes senescence	1.443	Abe, S., Nakashizuka, T., & Tanaka, H. Effects of canopy gaps on the demography of the subcanopy tree *Styrax obassia*. *Journal of Vegetation Science***, 9(6),** 787–796. (1998).
Swietenia macrophylla	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 *Swietenia macrophylla*. *Journal of Applied Ecology*, **45(6),** 1770–1779. (2008).
Syzygium jambos	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. *Journal of Applied Ecology*, **45(6)**, 1639–1648. (2008).
Taxus floridana	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, *Taxus floridana*. *Conservation Biology*, **18(2),** 432–443. (2004).
Tetraberlinia bifoliolata	Plantae	Escapes senescence	1.452	Norghauer, J. M., & Newbery, D. M. Seed fate and seedling dynamics after masting in two African rain forest trees. *Ecological Monographs***, 81(3),** 443–469. (2011).
Tsuga canadensis	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 (*Tsuga canadensis L.*). *Forest Ecology and Management*, **212(1-3**), 50–64. (2005).
Vatica mangachapoi	Plantae	Displays senescence	0.278	Hu; Wang. *Acta Ecol Sin*. (1988).

Vochysia ferruginea	Plantae	Displays senescence	0.641	Boucher, D. H., & Mallona, M. A. Recovery of the rain forest tree *Vochysia ferruginea* over 5 years following Hurricane Joan in Nicaragua: a preliminary population projection matrix. Forest *Ecology and Management*, **91(2-3),** 195–204. (1997).
Astragalus bibullatus	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. *Biological Conservation.* **203,** 243-251. (2016).
Centaurea corymbose	Plantae	Displays senescence	0.456	Hadjou Belaid, A. *et al.* Predicting population viability of the narrow endemic Mediterranean plant *Centaurea corymbosa* under climate change. *Biological Conservation*. **223,** 19-33. (2018).
Melocatus bahiensis	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. *Brazilian Journal of Botany*. **41(3),** 631-640. (2018).
Melocatus ernestii	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. *Brazilian Journal of Botany*. **41(3),** 631-640. (2018).
Verticordia fimbrilepsis	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 *Verticordia fimbrilepis subsp. fimbrilepis* in a fragmented landscape. *Plant Ecology*. **211(2),** 305-319. (2010).
Caladenia argocalla	Plantae	Displays senescence	0.664	Tremblay, R. L. *et al.* Population dynamics of *Caladenia*: Bayesian estimates of transition and extinction probabilities. *Australian Journal of Botany*. **57(4),** 351. (2009).
Caladenia elegans	Plantae	Displays senescence		Tremblay, R. L. *et al.* Population dynamics of *Caladenia*: Bayesian estimates of transition and

			0.820	extinction probabilities. *Australian Journal of Botany*. **57(4),** 351. (2009).Journal of Botany, 57(4), 351.
Caladenia macroclavia	Plantae	Displays senescence	0.652	Tremblay, R. L. *et al.* Population dynamics of *Caladenia*: Bayesian estimates of transition and extinction probabilities. *Australian Journal of Botany*. **57(4),** 351. (2009).
Cirsium pitcher	Plantae	Displays senescence	0.687	Halsey, S. J., Bell, T. J., McEachern, K., & Pavlovic, N. B. Population-specific life histories contribute to metapopulation viability. *Ecosphere.* 7(11), 15-36. (2016).
Cyrtandra dentata	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, *Cyrtandra dentata*. *Journal of Applied Ecology*. **54(5),** 1469-1477. (2017).
Dendrophylax lindenii	Plantae	Escapes senescence	1.051	Raventos J., Gonzalez, E., Mujica, E., & Doak, D. F. Population Viability Analysis of the Epiphytic Ghost Orchid (*Dendrophylax lindenii*) in Cuba. *Biotropica.* **47(2),** 179-189. (2015).
Echinacea angustifolia	Plantae	Escapes senescence	1.013	Dykstra, PhD thesis, 2013.
Frasera speciose	Plantae	Displays senescence	0.049	Che-Castaldo, J. P., & Inouye, D. W. The effects of dataset length and mast seeding on the demography of *Frasera speciosa*, a long-lived monocarpic plant. *Ecosphere*. **2(11),** 126. (2011).
Lepanthes rubripetala	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? *Biodiversity and Conservation.* **19(3)**, 637-650. (2009).
Vella pseudocytsus	Plantae	Displays senescence		Lozano, F. D., Saiz, J. C. M., & Schwartz, M. W. Demographic

paui			0.916	modeling and monitoring cycle in a long-lived endangered shrub. *Journal for Nature Conservation*. **19(6),** 330-338. (2011).
Zamia inermis	Plantae	Escapes senescence	1.820	Octavio-Aguilar, P. *et al.* Extinction risk of *Zamia inermis*: a demographic study in its single natural population. *Biodiversity and Conservation.* **26(4),** 787-800. (2017).

Supplementary Methods: 'R' computer code to extract age trajectories of fertility and mortality from population projection matrices, and to calculate Keyfitz' entropy.

```
#Code to quantify lx, mx and H, as calculated in:
#Senescence: Still an Unsolved Problem of Biology
#Mark Roper, Pol Capdevila & Roberto Salguero-Gómez
#Submitted to Nature.
#Code adapted by P.Capdevila (University of Oxford) and M.Roper (University of Oxford) from Jones et al. Diversity of ageing across the tree of life. Nature. 2014.
#Email: Mark Roper <mark.roper@keble.ox.ac.uk>
#Using equations from H. Caswell (2001) Matrix Population Models. 2nd Edition. #Sinauer, Sunderland, MA. Specific equations and pages within the references are #cited in each of the functions below.
#Last modified: June 18th, 2019
#Packages necessary:
require(MASS, popbio, popdemo)
###Functions
#Function to trim down lx and mx at a given percentage before stationary convergence (See Methods).
qsdConvergence <- function(survMatrix, beginLife){
  uDim <- dim(survMatrix)
  eig <- eigen.analysis(survMatrix)
  qsd <- eig$stable.stage
  qsd <- as.numeric(t(matrix(qsd / sum(qsd))))
#Set up a cohort
```

```
 nzero <- rep(0, uDim[1]) #Set a population vector of zeros
 nzero[beginLife] <- 1 #Set the first stage to =1
 n <- nzero #Rename for convenience
#Iterate the cohort (n= cohort population vector, p = proportional structure)
 dist <- p <- NULL
 survMatrix1 <- survMatrix
 for (j in 1:1500){ #j represent years of iteration
  p <- n / sum(n) #Get the proportional distribution
  dist[j] <- 0.5 * (sum(abs(p - qsd)))
  n <- survMatrix1 %*% n #Multiply the u and n matrices to iterate
 }
 #Find the ages for convergence to 0.1, 0.05, and 0.01
 pick1 <- min(which(dist < 0.1))
 pick2 <- min(which(dist < 0.05))
 pick3 <- min(which(dist < 0.01))
 convage <- c(pick1, pick2, pick3)
 return(convage)
}

#Function to determine probability of reaching reproduction, age at maturity and reproductive lifespan (Code adapted from H. Caswell's matlab code):
lifeTimeRepEvents <- function(matU, matF, startLife = 1){
uDim <- dim(matU)[1]
surv <- colSums(matU)
repLifeStages <- colSums(matF)
repLifeStages[which(repLifeStages>0)] <- 1
if(missing(matF) | missing(matU)){stop('matU or matF missing')}
if(sum(matF,na.rm=T)==0){stop('matF contains only 0 values')}

#Age at first reproduction (La; Caswell 2001, p 124)
D <- diag(c(Bprime[2,]))
Uprimecond <- D%*%Uprime%*%ginv(D)
expTimeReprod <- colSums(ginv(diag(uDim)-Uprimecond))
out$La <-  expTimeReprod[startLife]
}
```

```
#Function to create a life table
makeLifeTable<-function(matU, matF = NULL, matC = NULL, startLife = 1, nSteps = 1000){
 matDim <- ncol(matU)
  #Age-specific survivorship (lx) (See top function on page 120 in Caswell 2001):
  matUtemp <- matU
  survivorship <- array(NA, dim = c(nSteps, matDim))
  for (o in 1:nSteps){
    survivorship[o, ] <- colSums(matUtemp %*% matU)
    matUtemp <- matUtemp %*% matU
  }

  lx <- survivorship[, startLife]
  lx <- c(1, lx[1:(length(lx) - 1)])

#Start to assemble output object where we will store the data
 out <- data.frame(x = 0:(length(lx)-1),lx = lx)

  if(!missing(matF)){
    if(sum(matF,na.rm=T)==0){
      warning("matF contains only 0 values")
    }
#Age-specific fertility (mx, Caswell 2001, p. 120)
ageFertility <- array(0, dim = c(nSteps, matDim))
fertMatrix <- array(0, dim = c(nSteps, matDim))
matUtemp2 <- matU
e <- matrix(rep(1, matDim))
for (q in 1:nSteps) {
fertMatrix <- matF %*% matUtemp2 * (as.numeric((ginv(diag(t(e) %*% matUtemp2)))))
ageFertility[q, ] <- colSums(fertMatrix)
matUtemp2 <- matUtemp2 %*% matU
}
mx <- ageFertility[, startLife]
 mx <- c(0, mx[1:(length(mx) - 1)])
out$mx <- mx
}
```

```
##Calculations from COMPADRE and COMADRE
#Upload COMPADRE and COMADRE
load("COMADRE_v.3.0.0.RData")
load("COMPADRE_v.5.0.0.RData")
indexPopCOMADRE=1:dim(comadre$metadata)[1]
indexPopCOMPADRE=1:dim(compadre$metadata)[1]
allPopIndex<- c(indexPopCOMADRE,indexPopCOMPADRE)
###Loop to obtain demographic quantities
longPop<- dim(compadre$metadata)[1]
output<- data.frame("SpeciesAccepted"<- rep(NA,longPop),
          "MatrixDimension"<- rep(NA,longPop),

          "H"<- rep(NA,longPop),
          "La"<- rep(NA,longPop),
          "lx"<- rep(NA,longPop),
          "ux"<- rep(NA,longPop),
          "mx"<- rep(NA,longPop))

#Start the loop to make the calculations
for (i in 1:longPop){
index<- allPopIndex[i]
if (i<=length(indexPopCOMADRE)) {d=comadre} else {d=compadre}
#Define the name of the species
output[i,c("SpeciesAccepted")]<- unlist(lapply(d$metadata[index,c("SpeciesAccepted")], as.character))
#The calculations here employed define the beginning of life when an individual become established.
#Thus, we do not consider transitions from the "prop" stages
lifeStages<- d$matrixClass[[index]][1]
output[i,"stages"]=paste0(d$matrixClass[[index]][2])
notProp<- min(which(lifeStages != "prop"))
dorm<- which(lifeStages=="dorm")
matU<- d$mat[[index]]$matU
matU[is.na(matU)] <- 0
matF<- d$mat[[index]]$matF
matF[is.na(matF)] <- 0
matC<- d$mat[[index]]$matC
matC[is.na(matC)] <- 0
```

```
matA<- matU+matF+matC
#Store matrix dimension
output$MatrixDimension[i]=matDim=dim(matU)[1]
#Convergence to the quasi-stationary distribution
QSD <- qsdConvergence(matU,notProp))
#Calculate the life table
lifeTable <- makeLifeTable(matU,matF,matC,notProp,1000)[1:QSD[2],])
#Calculate and store Age at sexual maturity La
La  <- output[i, "La"] <- lifeTimeRepEvents(matU,matF,notProp)
#Survival curve
output[i,"lx"][[1]] <- list(unlist(lifeTable$lx[1:QSD[2]]))
#Survival with the beginning of lx set at age at maturity
output[i,"lxs"][[1]] <- list(unlist(lifeTable$lx)[La:QSD[2]])
#Fertility curve
output[i,"mx"][[1]] <- list(unlist(lifeTable$mx)[1:QSD[2]])
#Fertility curve setting the beginning at age at maturity
output[i,"mxs"][[1]] <- list(unlist(lifeTable$mx)[La:QSD[2]])
#Define age
output[i,"x"][[1]] <- list(unlist(lifeTable$x)[1:QSD[2]])
#Define age since starting at age at maturity
output[i,"xs"][[1]] <- list(unlist(lifeTable$x)[La:QSD[2]])
#Keyfitz' entropy estimation
output$H[i] <- as.numeric(-
t(lx[is.na(lx)==FALSE])%*%log(lx[is.na(lx)==FALSE])/sum(lx[is.na(lx)==FALSE]))
}
```

Source data

COMADRE_v.3.0.0 (as file)

COMPADRE_v.5.0.0 (as file)