1 **Old and ancient trees are life history lottery winners and act as evolutionary buffers**

2 **against long-term environmental change**

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19 **<u>Abstract</u>**

20 Trees can live many centuries with sustained fecundity and death is largely stochastic.

21 We use a neutral stochastic model to examine the demographic patterns that emerge over

22 time, across a range of population sizes and empirically observed mortality rates. A small

23 proportion of trees (~1% at 1.5% mortality) are life-history 'lottery' winners, achieving

24 ages >10-20x median age. Maximum age increases with bigger populations and lower

25 mortality rates. One quarter of trees (~24%) achieve ages that are 3-4 times greater than

26 median age. Three age classes (Mature, Old, and Ancient) contribute unique historical

27 diversity across complex environmental cycles. Ancient trees are an emergent property

28 of forests that requires many centuries to generate. They rradically change generation

29 time variance and population fitness, bridging infrequent environmental cycles. These

30 life-history 'lottery' winners are vital to future forest dynamics and invaluable data about

31 environmental history and individual longevity. Old-growth forests contain trees that

32 cannot be replaced through restoration or regeneration in the near future. They simply

33 must be protected to preserve their unique diversity.

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Old Trees in Nature

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46   Human cultures around the world have revered ancient trees as powerful spiritual

47   beings, connecting Earth and Heaven, as sources of wisdom, fertility, balance, and

48   longevity [1]. These myths and legends are often embodied by a particularly old and

49   venerated individual tree of exceptional presence, distinguishable from the many other

50   large trees in the forest. These ancient trees are seen as belonging to a separate and special

51   class of being that transcends the normal plane of existence, binding the tree to a deep

52   knowledge and awareness of history, change, and persistence. With increasing knowledge

53   about the role old trees play in ecosystems, biologists are also beginning to attach special

54   significance to individual ancient trees in populations [2, 3].

55   The ecological importance of old trees in forested ecosystems has been extensively

56   documented, particularly as small natural features that provide a wide range of services

57   [4–6]. And yet, our understanding of tree age structure in forested ecosystems remains poor

58   [7]. Fundamentally, the lifespan of even an ordinary tree exceeds the duration of long-term

59   ecological projects, so demographic studies of trees can only be performed on a cross-

60   sectional, not longitudinal, basis. Additionally, several inherent difficulties exist for the

61   reliable dating of old trees [8, 9]. Among tropical tree species in aseasonal climates, growth

62   rings are not tightly linked to annual cycles, making temporal dynamics difficult to

63   interpret [10-11]. Overall, the most reliable methods require complex – time consuming -

64   studies and these are rare at the population or community level [12].

65   Annual mortality rates have been estimated and measured at the population or

66   community level in many forests. These rates range from 0.3% to 5% for large mature

67   well-established individuals [13–19], often centered around 1.5-2%. While individual-based

68   stochastic models of tree mortality are commonly used to explore community ecological

69   and structural dynamics [7], the evolutionary implications of extreme longevity of

70   individuals have not previously been noted or explored. Using a neutral stochastic

71   mortality model, we obtain results that closely match those obtained through empirical

72   studies [20–22]. Here, we highlight several exceptional population-level demographic

73   properties that emerges from a neutral mortality model based upon empirical studies and

74   discuss their evolutionary implications, particularly given long-term environmental

75   cycles.

76   First, a very small proportion of individuals win the longevity "lottery" and obtain

77   exceptional ages, >>10 times greater than the median age in the population (Figure 1A).

78   These ancient trees are observed in natural populations and are possible because of the

79   lack of programmed senescence enabled by the woody plant growth form [3] and the low

80   mortality rates observed in many old growth forests globally [13–16]. We argue that despite

81   the rarity of these individuals, they play a significant role maintaining diversity in the

82   population and bridging across unusual and infrequent environmental conditions.

83   Second, a larger proportion of individuals reach significant ages many times greater than

84   the median age. These old individuals contribute substantially to the stabilization of

85   population diversity to intermediate environmental change. We objectively identify three

86   age classes ("mature", "old", and "ancient", see Methods for classification technique),

87   examine the properties of these groups in response to variation in population size and

88   mortality rate, and explore how each group relates to both short-term and long-term

89   environmental changes.

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91   **Modeling tree evolutionary demographics**

92   Mature, well-established trees are not programmed to senesce at a particular size or

93   age but instead die in consequence of serious damage due to abiotic factors, such as fires

94   or severe storms or sustained poor environmental conditions. In our model, we assume

95   that established canopy trees would survive until stochastic death causes mortality. We

96   are only modeling mature established trees and not seedlings, which are known to

97   experience very high mortality rates. We explore these demographic dynamics across a

98   range of basic parameters for annual mortality rate (0.1, 0.5, 1.0, 1.5, 2.0, 3.0, and 5.0%);

99   and population size (100, 1K, 10K, 100K, and 500K individuals); given a time span of

100   15K years. Population sizes are held stable throughout the simulation, assuming a mature

101   old-growth forest where space is fully occupied and community size constrained.

102   Population age refers to the length of time after establishment of the first cohort of mature

103   trees. Twenty-five replicates were run for each set of model parameters and results reflect

104   the average among replicates. These simulations are neutral in process to examine the

105   understanding patterns that emerge, given the basic assumptions of the model (see

106   Methods for more detailed description of the process). Code was written in Mathematica

107   12 (see Supplementary Material).

108   The existence of life history 'lottery' winners is apparent in all model conditions,

109   but the maximum age reached increases dramatically as mortality rate declines below 2%

110   (Fig. 1A), with a doubling of maximum age between 1% and 0.5% mortality. This range

111   of mortality rates corresponds directly to empirical values estimated from global forests,

112   indicating the small changes in forest mortality can have dramatic impact on the potential

113   age of trees in that forest. Additionally, maximum age does respond to increasing

114   population size but this effect declines for very large populations, with the most dramatic

115   response occurring among smaller populations, indicating the sensitivity of small forest

116   fragments to this process. Median population age, on the other hand, is insensitive to

117   population size but declines sharply with increasing mortality rate (Fig. 2). The mean

118   age of old also increases with declining mortality rate and increasing population size,

119   although less dramatically. Interestingly, the proportion of Old Trees in the population

120   (~24.4%) remains constant across all model conditions while the proportion of Ancients

121   remains constant for a particular mortality rate (e.g. ~1% of population for 1.5%

122   mortality) but increases with declining mortality (e.g. ~1.5% of population for 1%

123   mortality compared to 0.2% of population for 5% mortality). The Ancient trees,

124   particularly the oldest, display the greatest degree of responsiveness to changing model

125   conditions.

126   Our models also provide an objective estimate of the time required for a forest to

127   reach climax age, following the establishment of an even-aged cohort. This situation

128   resembles what happens managed restoration or natural regeneration after catastrophic

129   fire or storm or anthropogenic conversion. The climax age of a forest is a linear

130   relationship between Log[population size] and mortality rate (Fig. 1B), taking several

131   centuries given intermediate population sizes and mortality rates below 2%. We define

132   this climax age as the point where the age structure of the population stabilizes

133   (Supplementary Material 1) and the forest becomes older than the oldest surviving

134   individual. This moment in forest evolution also corresponds closely to when the oldest

135   individual becomes the lone representative of its age. These patterns have relevance to

136   many modern forests, particularly in the northern temperate regions, where even-aged

137   stands have grown in abandoned agricultural lands. Given prevalent natural mortality

138   rates, the climax status of the forest remains centuries in the future. With increased

139   mortality rates observed in forests around the world, these dynamics may be accelerated

140   and the potential for the emergent ancient age groups may be impossible.

141   We defined threshold ages for three age groups (Mature, Old, and Ancient) based

142   upon the properties of the rank-age distribution of the populations, after the population

143   had reached climax age (Supplementary Material 2). While the mature and old age

144   groups remain consistent across model conditions, we would highlight the variability and

145   sensitivity of the ancient age group to changes in mortality rate. Some individuals obtain

146   truly astonishing ages in relation to the mean age of the oldest individual, which as noted

147   above, is already substantially greater than median population age and even the median

148   oldest individual across replicates (Fig. 3). Even in the smallest populations (Fig. 2),

149   individuals achieve ages that are significantly more than the mean maximum age and the

150   frequency and magnitude of these outliers increase with declining mortality. Essentially,

151   a life-history lottery winner can emerge at any time point. The maximum age obtained

152   by these lottery winners is substantially greater than even forest climax age, indicating

153   that even after population age structure has stabilized, the ancient trees continue to

154   become more different and unusual for many more centuries. Unfortunately, the ancient

155   age group that emerges from a stochastic death process, and thus their impact on

156   evolutionary dynamics, can only be found in old-growth forests. Modern conversion

157   resets the long process.

158

159   **Buffering evolutionary change across different time scales**

160   Environmental change occurs on many different time scales and is an emergent

161   selection force that is composed of numerous factors of change. To explore the impact

162   of the three age groups on population level diversity, we constructed a scenario of

163   millennial environmental change, where fitness is determined by four different

164   underlying regular cycles (Fig. 4 and Supplementary Material 3). Given a mortality rate

165   of 1.5%, fitness diversity in each of the three age groups varies with increasing population

166   size in different ways. Compared to the overall distribution of fitness values present in

167   the environment over one thousand years, the Mature individuals correspond extremely

168   well with fitness values over the short-term but poorly with fitness averaged over the

169   entire time period. This distribution for Mature individuals does not change with

170   population size because this age group is present and consistent in all populations. The

171   Old individuals, on the other hand, closely match fitness diversity in the Mature group at

172   the smallest population size (Fig. 4a) but quickly shift until they closely match the

173   distribution of environmental variation. Fitness diversity among Ancient individuals

174   continues to shift with each change in population size. At the smallest population size,

175   Ancient individuals are entirely absent and as they appear, they are substantially different

176   than either of the two age groups and the environmental change. With increasing

177   population size and a corresponding increase in abundance and age of ancient individuals,

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178   their fitness diversity begins to converge on the distribution of overall environmental
179   variation (Fig. 4e).

180   The environmental scenario discussed here represents a single set of conditions for
181   the scale and frequency of environmental change and are thus only a case study but certain
182   lessons can be drawn from its results.   First, Mature individuals are present and
183   completely predictable in all populations, no matter the model parameters, although
184   median age does decline with increasing mortality rate. These Mature individuals are
185   constrained to environmental conditions experienced in the recent past. Secondly, the
186   Old individuals are also present and consistent in all but the smallest populations and
187   reflect the central tendency of environmental variation, given that the time scale of change
188   and the mean age of Old individuals roughly corresponds. Finally, the Ancient
189   individuals in intermediate sized populations can poorly fit both current and historical
190   environmental variation and represent a unique range of diversity compared to the other
191   age groups.

192   These Ancient trees can be a very valuable resource for the population as a whole,
193   if temporal scales of environmental variation extend beyond the age of old individuals,
194   thus bridging between extreme and infrequent environmental conditions that the
195   population might not survive without the ancient trees. Conversely, these ancient trees
196   might harbor traits and genes that are poorly fit to current and more short-termed
197   environmental change and if they dominated reproduction could reduce population
198   fitness. This could be particularly concerning if environmental change were directional,
199   moving steadily away from any central tendency. Ultimately, many other possible
200   environmental dynamics could be explored, particularly if environmental change is
201   directional and not constrained to a central value. Their rarity and difficult identification
202   makes discovery and direct study challenging using traditional ecological sampling
203   methods. Instead, the disproportionate and profound impact these ancient trees have on
204   the adaptiveness and sustainability of the population and species as a whole require an
205   innovative and specialized modeling approach. A full exploration of these dynamics
206   requires a comprehensive analytical approach to summarize results across a range of
207   environmental conditions to obtain general properties of this dynamic.

208   To assess the evolutionary buffering capacity of the emerging age class structure in
209   these populations, we examined variation in three estimators of generation time, given
210   different population sizes and mortality rates. The first estimator assumes that all
211   individuals alive in the population have an equal probability of producing successful

212 offspring.   The second estimator assumes that older individuals contribute
213 disproportionately to the next generation, based upon their age and not the number of
214 individuals of that age. The third estimator assumes that only the oldest individual alive
215 produces offspring. The first two estimators are basic methods of estimating generation
216 time while the last value indicates the maximum possible value for generation time in a
217 population over a given period of time.

218   Generation time for all three estimators increased with decreasing mortality rate,
219 with only slight changes in the first estimator but increased roughly sixfold for the last
220 estimator (Table 2). These values also changed dramatically with increasing population
221 size, increasing two- to three-fold within each mortality rate.   The first and third
222 estimators essentially represent the lower and upper bounds for generation time in the
223 population.   Given that selective environments change through a complex cyclical
224 process of several underlying patterns, extreme environmental conditions can return over
225 time periods of decades or hundreds of years (Figure 4A). Greater longevity of ancient
226 individuals increasingly bridges the temporal gap between the return of these
227 environmental extremes (Fig. 4B-E). If individuals that establish during those extreme
228 periods are more fit for those conditions, they can produce offspring that are likely to
229 have advantageous alleles that facilitate establishment during those extreme conditions.
230 Because fecundity is generally maintained in ancient trees, their contribution to
231 regeneration during these extreme but rare climatic conditions. Overall, despite the rarity
232 of the ancient individuals, each ancient individual is connected to a unique historical
233 circumstance (Fig. 4). They create a rich and deep genetic diversity within the community
234 that can bridge the gaps between rare and extraordinary environmental conditions.
235 Particularly, given predictions of global climate change, the baseline itself of cyclical
236 environmental change is shifting and the amplitude of change is increasing, driving
237 conditions towards more and more extreme values, further accentuating the importance
238 of these ancient reservoirs of valuable adaptive capacity at the outer margins of genetic
239 diversity. Beyond the neutral dynamics explored here, ancient trees also accumulate
240 heritable epigenetic imprinting and somatic mutations which further increase the overall
241 population diversity.

242

243 **Mechanisms to deal with aging in ancient trees**

244   Several mechanisms have evolved in individual trees to enable extreme longevity
245 and deal with negative effects of ageing (Fig. 4). In general, they can be grouped into

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246   two non-mutually exclusive categories: (i) senescence avoidance and (ii) aging tolerance.

247   "Senescence avoidance" includes either escaping from or preventing senescence.

248   Clonality in plants allows resetting the clock and escaping the wear and tear of ageing [23].

249   Although clonality is tightly linked to long lifespans, it only relates to the genotype, but

250   not the individual [3,24,25]. More relevant to the model presented here, ancient, non-clonal

251   trees usually show another mechanism to prevent aging for a very significant part of their

252   lifespan. Growth and senescence at two essential parts of the same coin. While plants are

253   growing, they cannot senesce. Senescence implies a reduction in vigour; therefore,

254   continuous growth is the most effective mechanism to prevent senescence. Several long-

255   lived plant species follow this strategy, including redwoods (*Sequoia sempervirens*),

256   which attain their maximum height at relatively advanced ages and generally do not show

257   a decline in vegetative growth vigour with increasing age [26]. This strategy has, however,

258   its limits. Due to functional leaf characteristics in redwoods, increasing leaf water stress

259   due to hydraulic and mechanical constraints may ultimately limit leaf expansion and

260   photosynthesis, thereby preventing further height growth beyond 130 meters even with

261   ample soil moisture [27]. Trees have evolved strategies to prevent death from water stress

262   once maximum height has been reached.

263   Stress tolerance is indeed a mechanism of aging tolerance, since it serves to delay

264   death as trees age. In ancient trees, the ability to maintain pluripotent meristems is key

265   for resistance (growth memory), resilience and stability of populations [28,29]. While shoot

266   apical meristems (SAMs) lead directly to vegetative and reproductive growth, axillary

267   meristems (AMs) are particularly important for plant branching and regeneration after

268   damage [30]. Ancient trees possess huge vegetative plasticity (Fig. 5), even through

269   epicormic shoots in consequence of severe disturbances [3].

270   In fact, the modular tree growth form, through both SAMs and AMs aboveground

271   and root apical meristem (RAMs) and lateral meristem (LMs) belowground, creates a

272   colony of competing genotypes that vary in their genotypic and phenotypic fitness

273   according to their historical development. The cambial meristem continually renews the

274   vascular system of the tree, responding to local conditions, both temporally and spatially,

275   essentially creating a record of change and resilience in the tree wood. Meristematic

276   tissues, both pluripotent and constantly renewing themselves, enable the tree to

277   essentially be potentially immortal [25]. This pluripotency is also observed in our ability to

278   propagate scion wood from old trees, which is often rejuvenated to some extent when

279   grafted onto a younger tree, truly enabling the possibility of potential immortality for a

280   particular genotype. Ultimately, the lack of separation between the germline and somatic

281   tissue allows the accumulation of heritable somatic mutations [31,32] but within-individual

282   selection at the meristem levels allows sweeping out of deleterious mutations and

283   selection for advantageous mutations below the individual level. Epigenetic imprinting

284   [33-35] across their canopies over centuries also allows them to be particularly good at

285   tolerating stress and preventing the wear and tear of aging and passing on advantageous

286   traits and phenotypes.

287

288   **Living stores of past selection and future adaptive capacity**

289   Abundant evidence suggests that trees can obtain extreme ages, well over a

290   millennium, due to their unique modular growth form and physiological plasticity and

291   that they regularly achieve ages of many centuries. A neutral stochastic death process, as

292   modeled here, produces population age structures that correspond to those observed in

293   natural populations. While the mature and old trees in the population are consistent across

294   model results, the properties of ancient trees only fully develop in large populations with

295   relatively low mortality rates after many centuries of forest growth. These ancient trees

296   reach ages substantially greater than other trees in the community and comprise a small

297   proportion of the total population. We argue that they play a significant and

298   underappreciated role in the evolutionary dynamics of forest tree species.

299   Critically, in converted forests or populations of very small size, the long

300   demographic tail of ancient trees is missing. Our results suggest that climax forest

301   containing ancient trees obviously requires several centuries, even when mortality rates

302   are relatively high (3%). Estimates that 'old-growth' forest can be achieved in 150 [36]

303   neglects the impact of ancient trees. These ancient trees are indicators of the degree of

304   development in old-growth processes [37]. Old and ancient trees are unique proxies for

305   reconstructing past climate and environment [38]. Such old trees have survived multiple

306   decadal (AMO and PDO generally lasting between 30-70 years) and even longer

307   contrasting climatic phases (Medieval warm period, Little ice age, global warming).

308   While our model assumes neutrality, the survivorship of some trees also indicates the

309   growth conditions where functional traits [39] confer resistance to biotic and abiotic

310   stresses. Our currently highly fragmented, largely converted global forests face profound

311   evolutionary challenges, given the loss of the buffering effect of ancient trees, particularly

312   in the face rapidly emerging novel environments expected for the Anthropocene. Once

313 disturbed by man, a regeneration forest needs a millennium to recover its natural stock of
314 ancient trees.

315 Finally, ancient trees represent a major reservoir for deep genetic diversity that can
316 bridge long temporal gaps between extreme environmental conditions. While these
317 ancient individuals are relatively infrequent in the population, their existence in the
318 community can have profound impacts on the evolutionary dynamics, particularly
319 regarding coalescent and lineage sorting processes, which are both defined by generation
320 time [40,41]. Given our poor understanding of demographics or population dynamics in
321 forest trees, the impact of possible variation in generation time, caused by skewed or
322 unusual demographic structures [42-44] is not frequently considered. We demonstrate that
323 the presence in ancient trees in the community greatly extends generation time and greatly
324 increases its variance, thus also extending and increasing the variance in coalescent times
325 and lineage sorting processes. While evidence of senescence, through diminished seed
326 output, has been recently reported [45], older trees often do contribute a disproportionate
327 number of seeds during a fruiting event [46] and no evidence exists in regard to their pollen
328 contribution. Their participation in population genetics of the community remains
329 significant, despite their rarity in the community. Empirically, tree genomes are often
330 noted for their high levels of heterozygosity and typically exhibit higher within
331 populations levels of genetic diversity in comparison to between population levels,
332 supporting this hypothesis. This suspended process of coalescence would also address
333 the paradox of fast microevolution but slow macroevolution [46].

334 For all of these reasons, old-growth forests with their unique stock of ancient trees
335 are becoming increasingly important to protect. Losing these trees is similar to allowing
336 species to go extinct. Ecologically, ancient trees are known to be unique biodiversity
337 hubs [47] that provide key or unique ecosystem functions unparalleled by managed forests.
338 They contribute disproportionately to the forest rate of carbon sequestration, as this rate
339 continuously increases with tree size [48]. But these ancient trees, perhaps most critically,
340 are an irreplaceable evolutionary resource for the tree species themselves. The loss of
341 these ancient trees can greatly reduce the evolutionary potential of the species. Preserving
342 and restoring ancient trees everywhere in the world, from the heart of old growth forests
343 to tiny fragments along roadsides, is an urgent goal for a sustainable future. We strongly
344 advocate research focused on these ancient trees and their contribution to the future
345 adaptive capacity of our global forests.

346

347   **Methods**

348

349   **Simulation model**

350   A simple technique for imposing a stochastic mortality rate on a population of

351   individuals with a constant number of individuals in the population was written in

352   Mathematica 12 for Mac OS (Wolfram Research). The simulation involves no spatial or

353   fitness component into the likelihood of death but instead all individuals are equally likely

354   to perish. The initial settings mimic recovery of a site after a complete conversion with

355   all individuals starting at the same time and same age. All individuals are considered

356   established once they appear in the population simulation with equal probability of

357   mortality.

358   Each step in the simulation is equivalent to a year and the dead individuals are

359   chosen randomly and then removed from the population, with the number of individuals

360   to be removed being the annual mortality rate multiplied times the population size.

361   Surviving individuals have a year added to their age and a new cohort of one year old

362   individuals replace the dead individuals removed from the population. This step is

363   repeated for the duration of the simulation model. All models were run for an equivalent

364   of 15000 years.

365   The parameters explored in the model vary by population size (100, 1000, 10K,

366   100K, and 500K individuals) and annual stochastic mortality rate (0.001, 0.005, 0.01,

367   0.015, 0.02, 0.03, and 0.05). Each set of parameters were examined across 25 replicates.

368   To explore the impact of increasing population size, one set of replicates were also run

369   for one million individuals given a mortality rate of 0.015. Little variation was observed

370   in the results and further exploration of a broader parameter space did not seem warranted.

371   The mortality rate of 0.02 appears to be a bit of a threshold as the results change quickly

372   below this rate but the lower bound of mortality studied here (0.001) does not appear

373   biological relevant as the results do not reflect empirical evidence from global forests or

374   other organisms which match this mortality model. More detailed exploration of the

375   impact of small population sizes on these dynamics is warranted, as the lower bound of

376   100 individuals generated unusual results and presented certain challenges to the model

377   effort.

378   To simplify the analysis of the demographic patterns, samples were taken of the

379   population every 100 years during the 15000 year time period and individuals were

380   grouped by age class. All subsequent analyses were performed on these demographic

381 tables. Given the initial conditions of the model, where an even-aged cohort of
382 individuals dominate the population in the beginning of the model but slowly go through
383 attrition until the youngest age class becomes the most abundant. We determined that
384 this point where the age class structure becomes stable represents the population climax
385 age, at which the impact of the reset no longer has an effect. Population climax age was
386 technically defined as the point at which the oldest age class is represented by a single
387 individual. These dynamics are explained in greater detail in the Supplementary Material
388 1. All analyses were performed after the demographic patterns became stable.

389

390 **Age group classification**

391 We detected an emerging group of individuals in our simulations that were
392 substantially older than the rest of the population. We deemed these individuals as
393 'ancient' and described them as life history lottery winners because they were always a
394 small fraction of the overall population but departed entirely from the population
395 characteristics, extending a very long and thin tail to the distribution of ages (see
396 Supplementary Material 2). Further exploration of the age-rank distribution revealed that
397 three separate segments of the population (mature, old, and ancients) could be identified
398 objectively by age, corresponding to the different parts of the age-rank curve. The
399 threshold between the mature and elder groups could be efficiently determined as twice
400 the age of the median age of the entire population. This threshold, easily calculated,
401 corresponds closely to the inflection point in the rank-age distribution where the steady
402 and linear progression becomes non-linear. The threshold age between old trees and
403 ancients was technically defined as the point where the subset of five consecutive ages
404 present in the population are separated by an average of two years, e.g. the sequence of
405 ages becomes 450, 452, 454, 456, 458. We found that applying this rule to different
406 population sizes resulted in different threshold ages for ancients, that increased with
407 population size, but the absolute number of individuals above this threshold remained
408 constant across population sizes. But, plotting this threshold on the rank-age distributions
409 revealed that it did not correspond well with the properties of the curve and only included
410 a very small portion of the obvious long tail of very old individuals. Instead, we found
411 that the 10K individual population appears to represent a point at which the dynamics
412 become predictable at larger population sizes. Setting the threshold for ancient age as the
413 point where the rule was accepted for 10K for all population sizes then fit the properties
414 of the curve.

13

415

416 **Exploring environmental fitness dynamics**

417 In order to explore the role of individuals in these different age groups given cyclical

418 environmental change, we simulated an environmental fitness value that is the summation

419 of four different cycles that recur over the time period of the simulation. Because of the

420 large possible parameter space given this type of model, we wrote a 'tunable' but arbitrary

421 equation that generated an emergent pattern that was appropriate to empirical patterns of

422 environmental cycles that occur on various temporal scales, from decades to millennia.

423 The equation is the summation of

424 4 (Sin[x*.01]) + Sin[x*wave1freq] + wave2amp*Sin[x*wave2freq] +

425   wave3amp*Cos[x/wave3freq];

426 where x = time and the variables wave#amp and wave#freq correspond to the

427 properties of the specific environmental cycle. These variables could be easily modified

428 and a representative set were chosen to examine the impact of the different age groups

429 over these fitness cycles. See Supplementary Materials 3 for a detailed description of the

430 process and the background for the background environmental fitness value used in

431 Figure 3.

432 To assess the impact of the different age groups on the adaptive capacity of the

433 population, we assumed that fitness determined the ability of the individual to establish.

434 Therefore, the individuals was assigned the fitness value present in the environment at

435 the time of its establishment. For illustrative purposes, a single sample point was chosen

436 arbitrarily for a single replicate (year 10300 in the tenth replicate) to examine the

437 distribution of fitness values for each age group. We feel this approach is adequate and

438 corresponds to our ability to collect empirical data on these types of long-lived

439 individuals, which is inherently latitudinal and not longitudinal in quality. Additionally,

440 this type of analysis is novel and protocols for exploring the properties of population

441 fitness would require the development of a new set of tools. This future work would be

442 required to comprehensively explore the full impact of different age groups across all

443 environmental situations but we feel that this effort is beyond the scope of the current
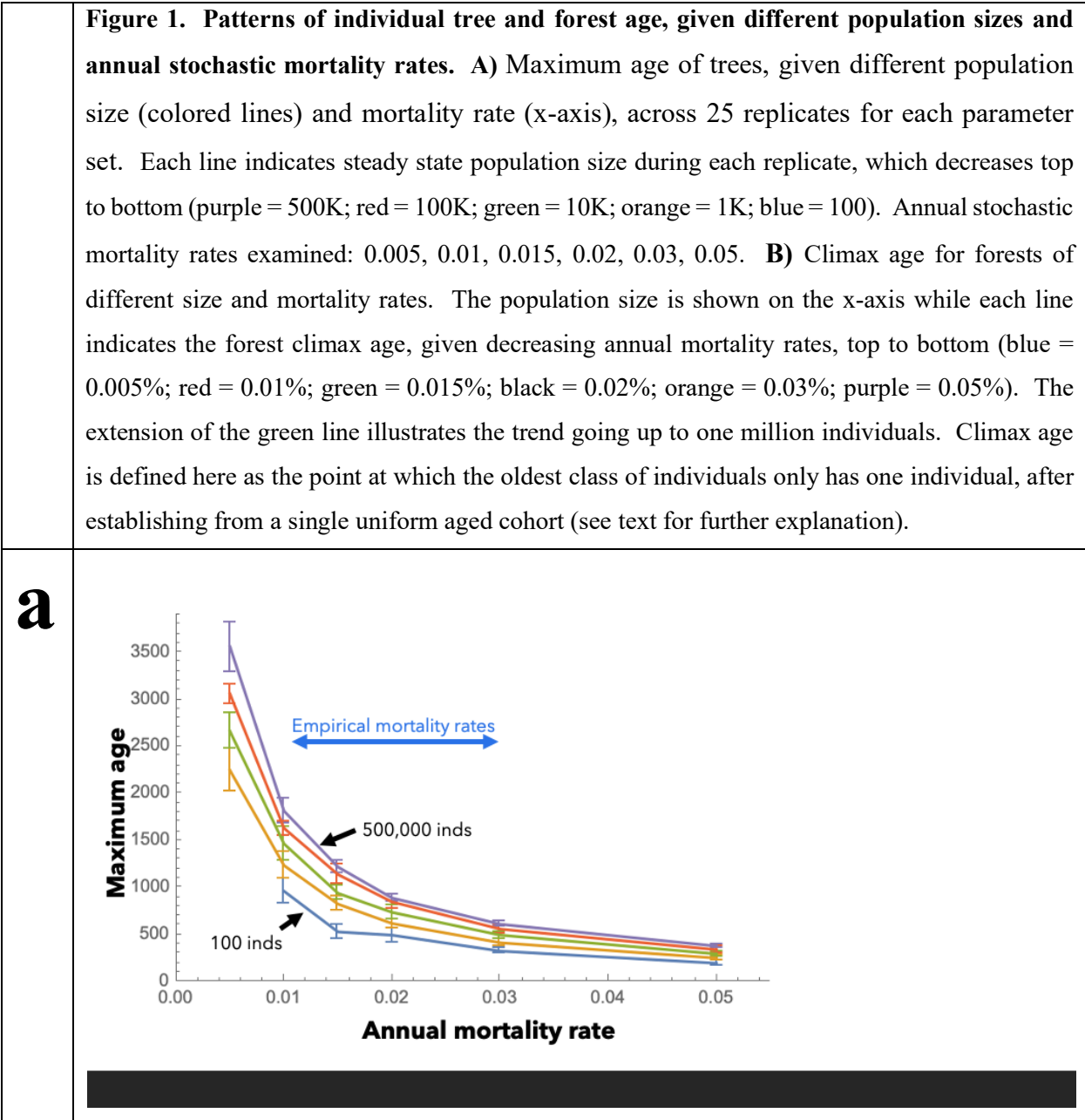
444 analysis.

445 The population descriptors of fitness for each age group were compared to the

446 overall background fitness value over 1000 years, across population sizes and mortality

447 rates.

448

449 **Estimation of generation time**

450

451   Generation time was estimated in three ways: 1) all living individuals in a cohort
452 have equal probability of contributing an offspring to the establishing cohort, regardless
453 of their age; 2) individuals in each age class have the same probability of contributing an
454 offspring to the establishing cohort, regardless of their abundance; and 3) only the oldest
455 living individual contributes to the establishing cohort. These three estimators were
456 calculated 1) by randomly choosing an individual from the last living cohort produced at
457 the end of a simulation which served as the 'tip' individual; 2) the time of establishment
458 for the tip individual was determined by subtracting the individual's age from the time of
459 sampling in the simulation; 3) the progenitor of the individual is selected based upon the
460 three criteria described above: i) randomly among all living individuals; ii) randomly
461 among all age classes present; and iii) the oldest living individual. Steps 2 and 3 were
462 repeated until the beginning of the simulation was reached, keeping track of the number
463 of individuals required to traverse the entire simulation, from the end to the beginning.
464 Generation time was then calculated by dividing the length of the simulation (15000
465 years) by the number of individuals required to span from beginning to end. This entire
466 process was repeated ten times for each of the 25 replicates, meaning that a total of 250
467 estimates for generation time were calculated for each combination of model parameters.

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Table 1. Variation in generation time, given different community sizes (rows) and mortality rates (columns). The values for each combination of parameters illustrate mean generation time assuming contribution to the next generation is i) equally among all individuals; ii) proportional to age class; and iii) only by the oldest individual, respectively. The first assumption estimates the average generation time if fecundity is equal across ages and establishment is stochastic. The second assumption estimates the average generation time if fecundity increases linearly with age and establishment is stochastic. The last assumption estimates the maximum possible generation time, given the presence of ancient individuals. Because the temporal resolution of the analysis is in one hundred year steps, the lowest value for generation time is 100 years. The value for one million individuals at 1.5% mortality is 299.

	1.0%			1.5%			2.0%			5.0%		
	i	ii	iii	i	ii	iii	i	ii	iii	i	ii	iii
100	121	121	449	102	103	206	102	103	207	<100	<100	<100
1000	121	159	649	106	125	432	102	111	319	<100	<100	105
10000	121	239	822	106	174	563	102	140	415	<100	100	136
100000	121	341	992	106	232	689	102	184	515	<100	103	198
500000	121	403	1121	106	281	776	102	218	588	<100	108	213

Figure 1. Patterns of individual tree and forest age, given different population sizes and annual stochastic mortality rates. A) Maximum age of trees, given different population size (colored lines) and mortality rate (x-axis), across 25 replicates for each parameter set. Each line indicates steady state population size during each replicate, which decreases top to bottom (purple = 500K; red = 100K; green = 10K; orange = 1K; blue = 100). Annual stochastic mortality rates examined: 0.005, 0.01, 0.015, 0.02, 0.03, 0.05. **B)** Climax age for forests of different size and mortality rates. The population size is shown on the x-axis while each line indicates the forest climax age, given decreasing annual mortality rates, top to bottom (blue = 0.005%; red = 0.01%; green = 0.015%; black = 0.02%; orange = 0.03%; purple = 0.05%). The extension of the green line illustrates the trend going up to one million individuals. Climax age is defined here as the point at which the oldest class of individuals only has one individual, after establishing from a single uniform aged cohort (see text for further explanation).
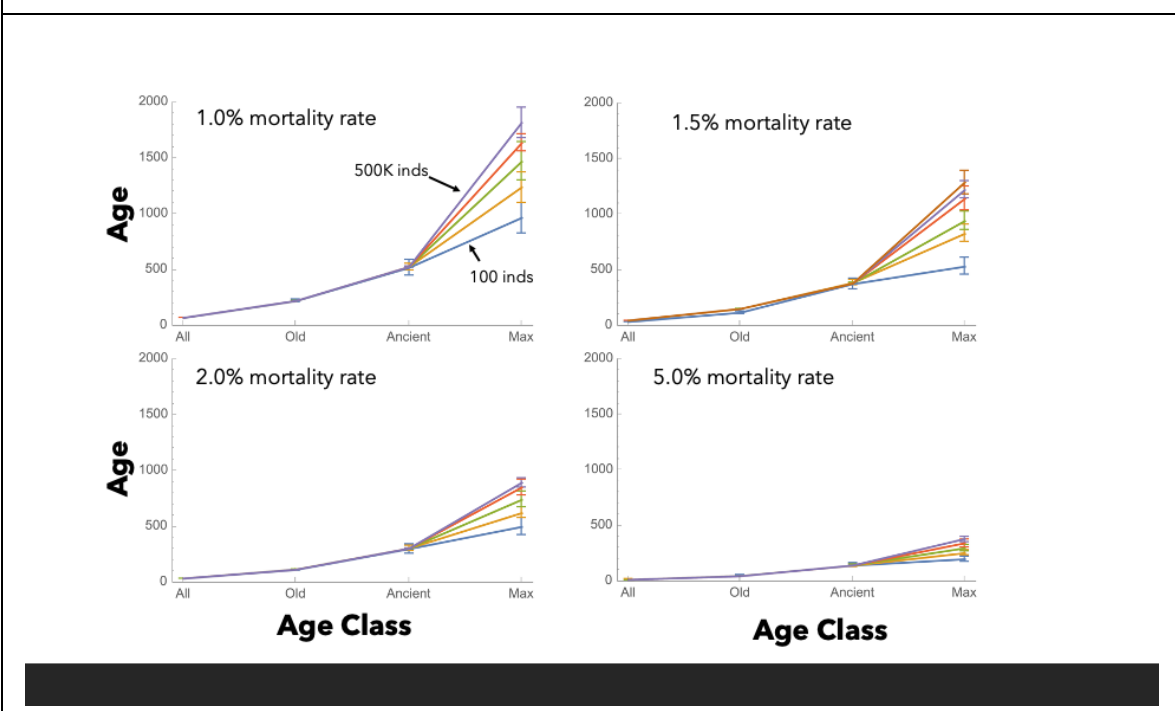
b

Figure 2. Mean age and standard deviation of different age classes, given different mortality rates and population sizes, across replicates. The lines connect models with different population sizes, with the smallest population size (100 inds) having the lowest maximum up to the largest population size (500K inds) with the highest maximum age.
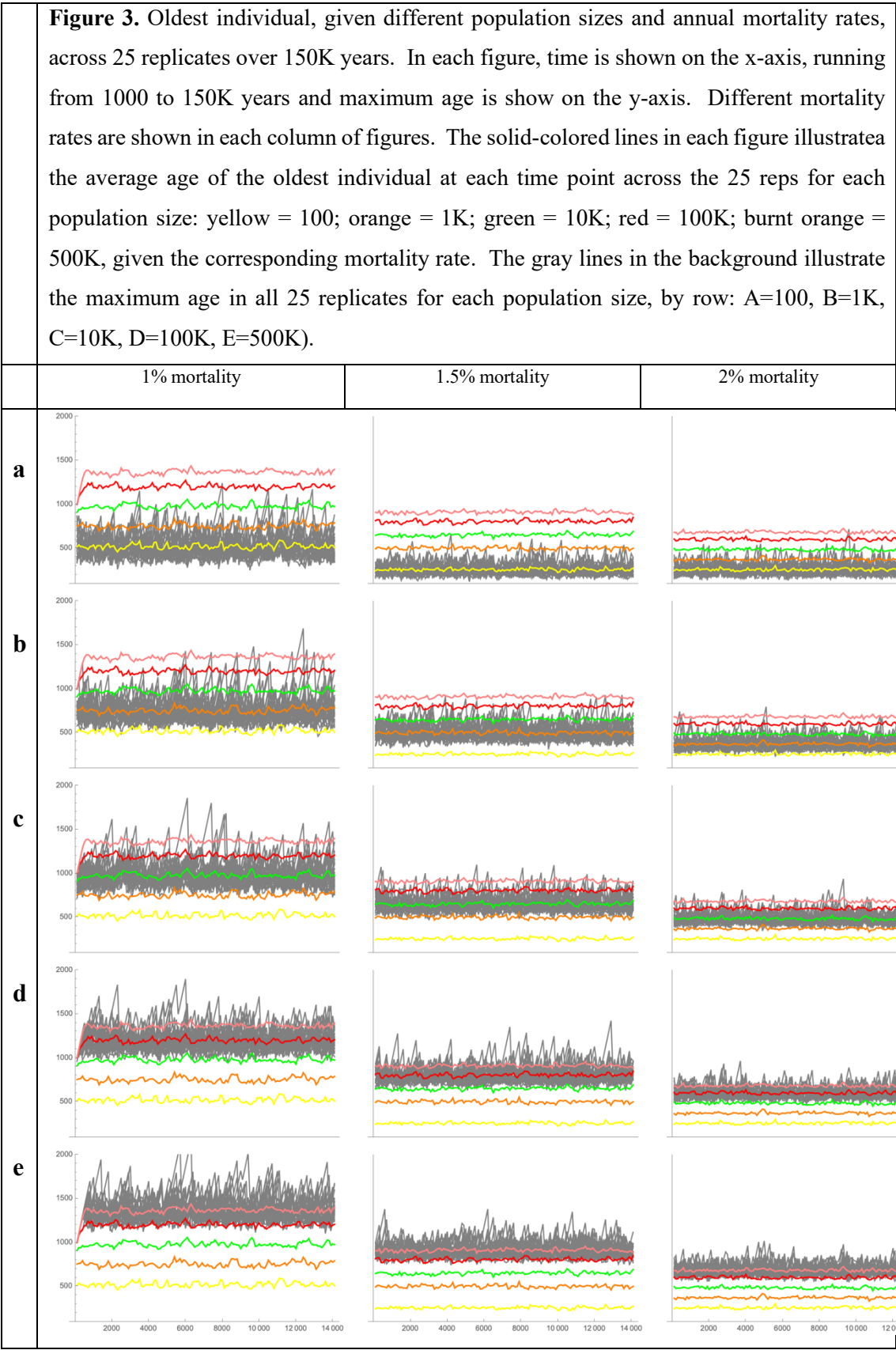

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Figure 3. Oldest individual, given different population sizes and annual mortality rates, across 25 replicates over 150K years. In each figure, time is shown on the x-axis, running from 1000 to 150K years and maximum age is show on the y-axis. Different mortality rates are shown in each column of figures. The solid-colored lines in each figure illustratea the average age of the oldest individual at each time point across the 25 reps for each population size: yellow = 100; orange = 1K; green = 10K; red = 100K; burnt orange = 500K, given the corresponding mortality rate. The gray lines in the background illustrate the maximum age in all 25 replicates for each population size, by row: A=100, B=1K, C=10K, D=100K, E=500K).

Figure 4. Representative population demographics and fitness through time, given an annual stochastic mortality rate of 1.5% and an environmental fitness that varies through time. Each row of figures corresponds to a different population size: a) 100, b) 1K, c) 10K, d) 100K, e) 500K. In the left column, the individual longevity of trees is shown by a line, running left to right, from the time of their establishment to the time. Lines are color-coded according to age group: green = mature; red = old; black = ancients (see Methods for technical definitions). Each figure represents the population of living individuals observed at a single sample time (10,300 years) from a single replicate. The sample time was chosen for illustration purposes. The environmental fitness value for all is shown by the red waveform populations (y-axis), which is the outcome of four underlying environmental patterns (see Supplemental material) changing through time (x-axis). In the right column, the descriptors of age group fitness are shown. The error bars illustrate the 25% quantile of population fitness, the lower central bar corresponds to population mean, the upper central bar corresponds to population median. The thin black errors bars illustrate the environmental fitness value over the one thousand year period, including the horizontal black line, which corresponds to the mean environmental fitness value over this time period.
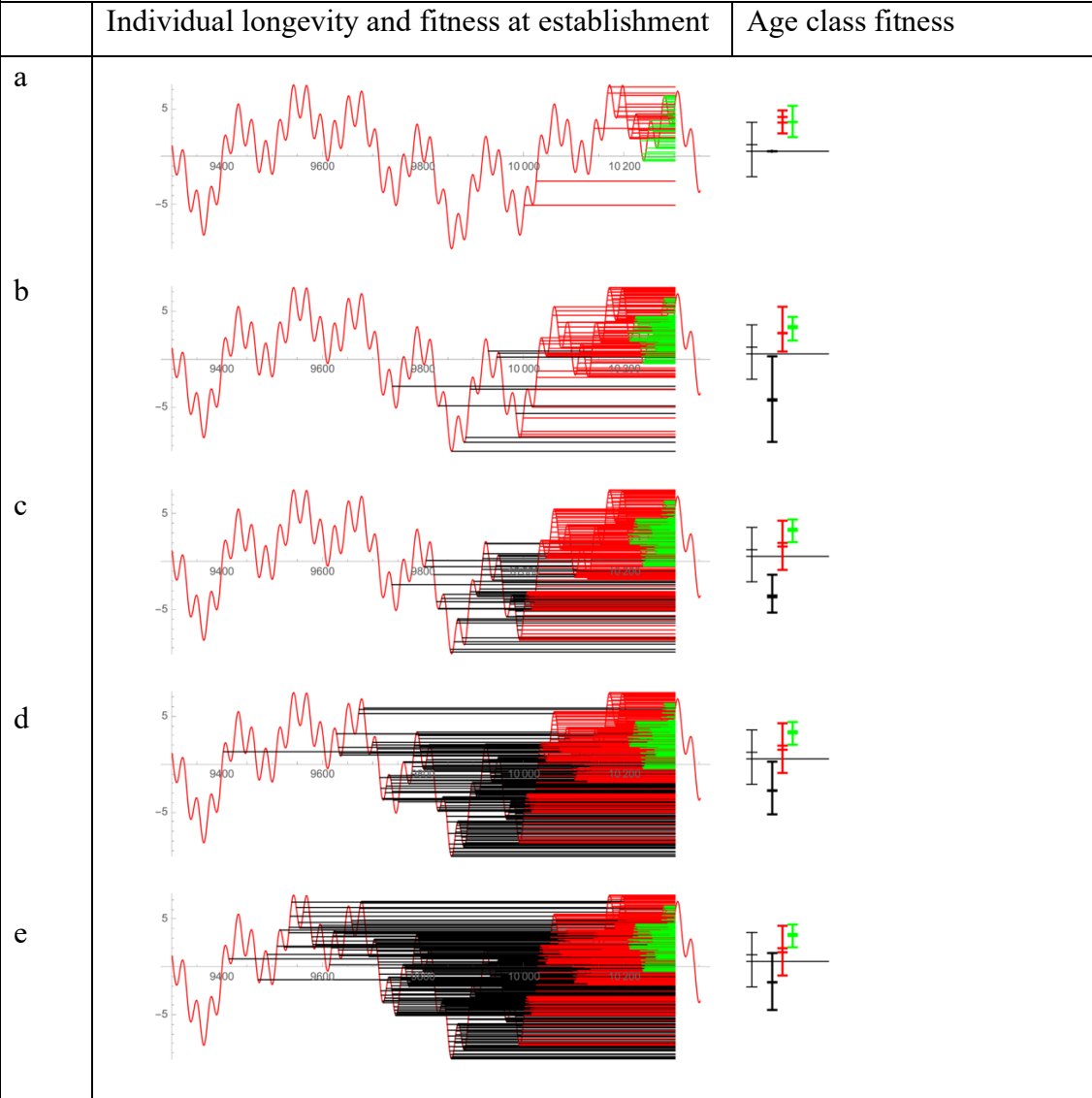
Figure 5. Major mechanisms evolved by ancient trees to defy aging. Lack of programmed senescence enables very long lifespans in trees and implies that death is largely due to stochastic events. The indeterminate life span of trees arise from a combination of mechanisms that serve both to prevent senescence (modularity, continuous growth, dormancy) and tolerate aging (stress tolerance), creating enormous potential and flexibility in longevity.
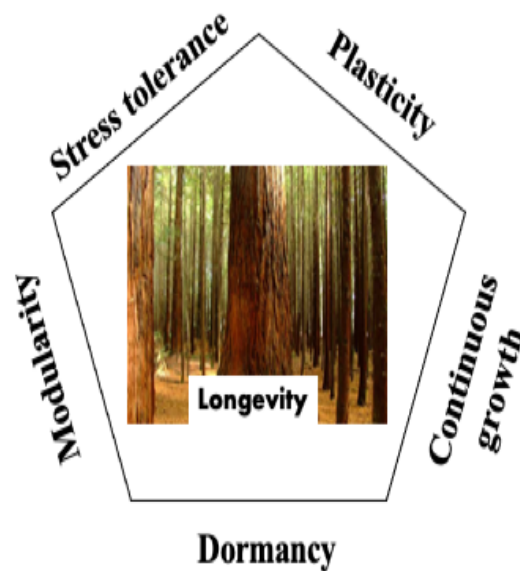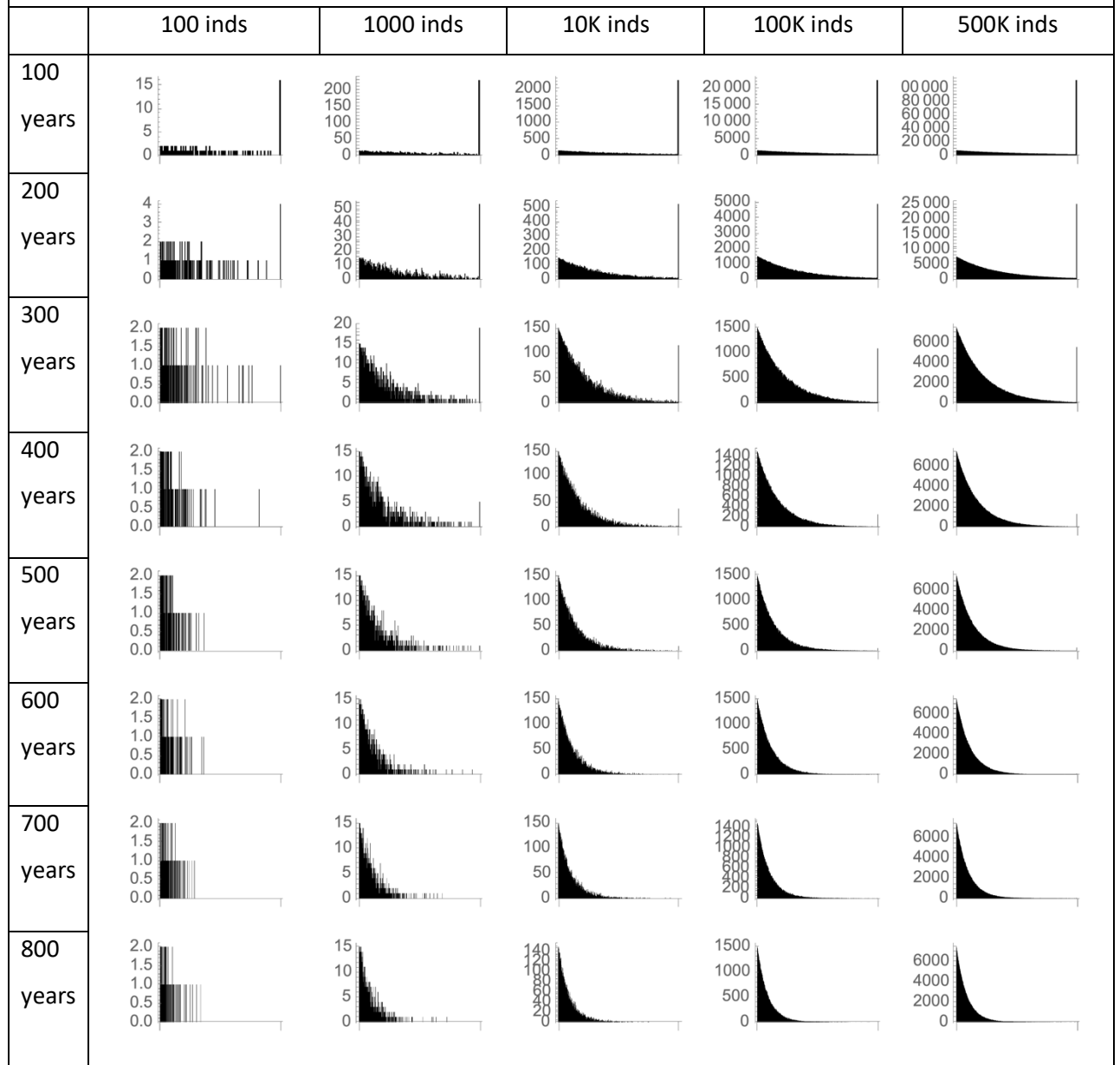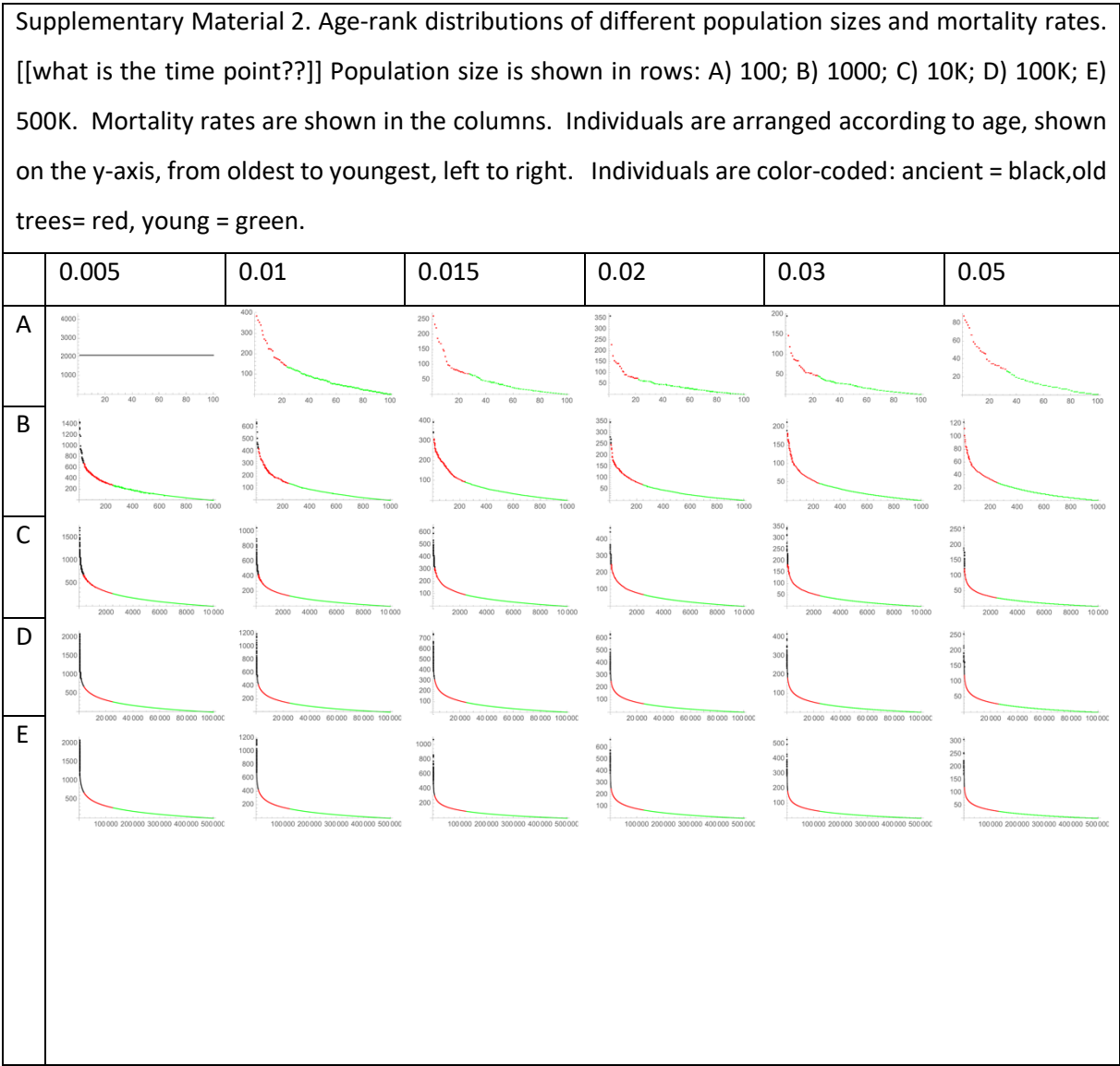
Figure 6. Canopy rejuvenation: epicormic branching after a severe crown disturbance in an old sessile oak (left side). Acorn production in a 600 yr old sessile oak trees in the Aspromonte National Park where the oldest dated temperate flowering tree in the world (930 yrs) is still fruiting (Piovesan et al. 2020).

Supplementary Material 1. Abundance of age classes in populations of different sizes with increasing population age, in 100 year increments, given an annual mortality rate of 1%. Columns show different population sizes and rows show increasing community age. In each figure, age classes are shown on the x-axis with a maximum value that equals the community age while abundance of individuals in each age class are shown on the y-axis. Values shown are from a single representative replicate.

Supplementary Material 2. Age-rank distributions of different population sizes and mortality rates. [[what is the time point??]] Population size is shown in rows: A) 100; B) 1000; C) 10K; D) 100K; E) 500K. Mortality rates are shown in the columns. Individuals are arranged according to age, shown on the y-axis, from oldest to youngest, left to right. Individuals are color-coded: ancient = black, old trees= red, young = green.

Supplementary Material 3. Exploring population level fitness, given multi-cyclical environmental change. Environmental change was modeled by adding four environmental cycles to create an emergent environmental cycle. The top panel shows the four underlying cycles in gray and emergent cycle in red. The bottom panel shows just the emergent cycle.
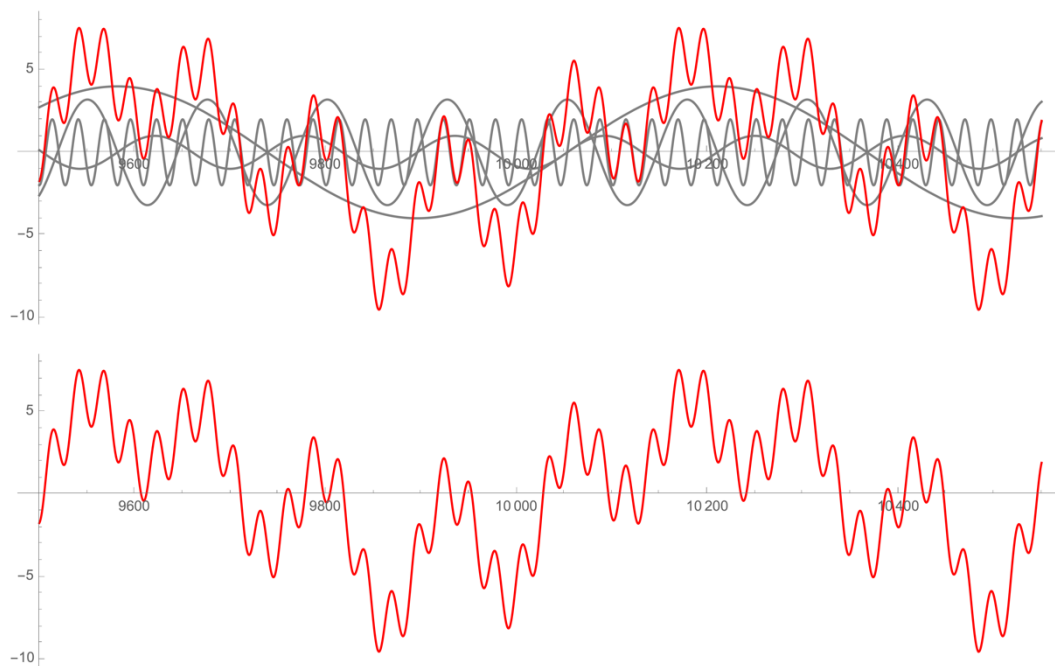
The functions describing the four underlying cycles are: 1) Sin[x*.01]); 2) Sin[x*wave1freq];

3) wave2amp*Sin[x*wave2freq]; and 4) wave3amp*Cos[x/wave3freq, where x = time point in simulation and wave#amp and wave#freq are variables describing the amplitude and frequency of the cycle.

Population fitness was estimated within a one thousand year time period to reflect a reasonable amount of environmental change during which each underlying cycle and the emergent cycle would go through several complete revolutions.

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Supplementary Material. Demographic patterns of populations given different mortality rates (rows) and population sizes (columns). The red line indicates the fluctuating fitness value determined by four interacting environmental cycles. The black lines represent the individuals alive at the end of the time series, originating at the time of their establishment, for each set of parameter conditions. This illustration represents one replicate and one time point.

	100 inds	1000	10000	100000	500000
.005					
.01					
.015					
.02					
.03					
.05					