



Old and ancient trees are life history lottery winners and vital evolutionary resources for long-term adaptive capacity

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Trees can live for many centuries with sustained fecundity and death is largely stochastic. We use a neutral stochastic model to examine tree demographic patterns that emerge over time, across a range of population sizes and empirically observed mortality rates. A small proportion of trees (~1% at 1.5% mortality) are life-history 'lottery winners', achieving ages >10–20× the median age. Maximum age increases with bigger populations and lower mortality rates. One-quarter of trees (~24%) achieve ages that are three to four times greater than the median age. Three age classes (mature, old and ancient) contribute unique evolutionary diversity across complex environmental cycles. Ancient trees are an emergent property of forests that requires many centuries to generate. They radically change variance in generation time and population fitness, bridging centennial environmental cycles. These life-history 'lottery' winners are vital to long-term forest adaptive capacity and provide invaluable data about environmental history and individual longevity. Old and ancient trees cannot be replaced through restoration or regeneration for many centuries. They must be protected to preserve their invaluable diversity.

Human cultures around the world have revered ancient trees as powerful spiritual beings, connecting Earth and Heaven, as sources of wisdom, fertility, balance and longevity¹. These myths and legends are often embodied by a particularly old and venerated individual tree of exceptional presence, distinguishable from the many other large trees in the forest. These ancient trees are seen as belonging to a separate and special class of being that transcends the normal plane of existence, binding the tree to a deep knowledge and awareness of history, change and persistence. With increasing knowledge about the role old trees play in ecosystems, biologists are also beginning to attach special importance to individual ancient trees in populations^{2,3}.

The ecological importance of old trees in forested ecosystems has been extensively documented, particularly as small natural features that provide a wide range of services^{4–6}. And yet, our understanding of tree age structure in forested ecosystems remains poor⁷. Fundamentally, the lifespan of even an average tree greatly exceeds the duration of any current ecological project, so true demographic studies of trees have never been carried out, except on a cross-sectional, not longitudinal, basis. Additionally, inherent difficulties exist for the reliable dating of old trees^{8,9}. Among tropical tree species in aseasonal climates, growth rings are not tightly linked to annual cycles, making temporal dynamics difficult to interpret^{10,11}. Overall, the most reliable methods require complex, time-consuming studies, rarely performed at the population or community level¹².

Annual mortality rates have been estimated and measured at the population or community level in many forests. These rates range from 0.3% to 5% for well-established individuals^{13–19}, often centred around 1.5–2%. While individual-based stochastic models of tree mortality are commonly used to explore community ecological and structural dynamics⁷, the evolutionary implications of extreme longevity of individuals have not been explored. In this Article, using

a neutral stochastic mortality model based on observed mortality rates, we obtain demographic results that closely match those obtained through empirical studies^{12,20–22}. Additionally, we highlight several exceptional population-level demographic properties that emerge from these models and discuss their evolutionary implications, particularly given long-term environmental cycles.

First, a small proportion of individuals win the life-history 'lottery' and obtain exceptional ages, far more than ten times greater than the median age in the population (Fig. 1a). These ancient trees are observed in natural populations and are possible because of the lack of programmed senescence enabled by the woody plant growth form³ and the low mortality rates observed in many old-growth forests globally^{13–16}. We argue that, despite the rarity of these individuals, they play a significant role maintaining diversity in the population and bridging across unusual and infrequent environmental conditions. Second, a larger proportion of individuals reach significant ages many times greater than the median age. These old individuals contribute substantially to the stabilization of population diversity to intermediate environmental change. Finally, we objectively identify three age classes ('mature', 'old' and 'ancient', see Methods for classification technique), examine the properties of these groups in response to variation in population size and mortality rate, and explore how each group relates to both short-term and long-term environmental changes.

Life-history lottery winners

Mature, well-established trees are not programmed to senesce at a particular size or age but instead die in consequence of serious damage due to external biotic and abiotic factors, such as pests and diseases, fires, wind and ice storms, or sustained poor environmental conditions. In our model, we only include mature established trees and assume that, once a tree becomes established, its death is entirely stochastic. Therefore, we are not modelling seedlings,

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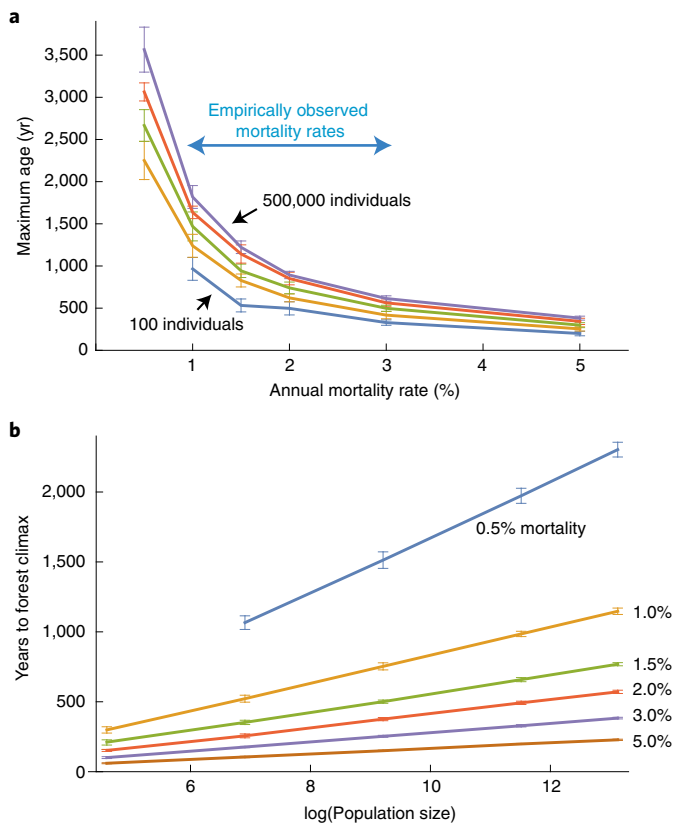


Fig. 1 | Maximum tree and forest climax age, given different population sizes and annual stochastic mortality rates. **a**, Maximum age of trees, given different population size (coloured lines) and mortality rate (x axis), across 25 replicates for each parameter set. Each line indicates steady-state population size during each replicate, which decreases from top to bottom (purple, 500,000; red, 100,000; green, 10,000; orange, 1,000; blue, 100). Annual stochastic mortality rates examined: 0.5%, 1.0%, 1.5%, 2.0%, 3.0%, 5.0%. Interval indicated by blue arrows illustrates the range of empirical mortality rates observed in mature forests. **b**, Climax age for forests of different size and mortality rates. The log-normal 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, 0.5%; red, 1.0%; green, 1.5%; black, 2.0%; orange, 3.0%; purple, 5.0%). Climax age is defined here as the point at which the oldest class of individuals only has one individual, after establishing from a single uniformly aged cohort (Methods).

which are known to experience very high mortality rates. We impose a range of annual mortality rates (0.1%, 0.5%, 1.0%, 1.5%, 2.0%, 3.0% and 5.0%), which reflect mortality rates observed in natural forests, as discussed above. Each model run lasts 15,000 years and populations are sampled every 100 years. Population sizes are held stable throughout the simulation, assuming an old-growth forest where space is fully occupied and community size constrained, and population sizes modelled include 100, 1,000, 10,000, 100,000 and 500,000 individuals. Twenty-five replicates were run for each set of model parameters and results reflect the average among replicates. These simulations are neutral in process to examine the understanding patterns that emerge, given the basic assumptions of the model (see Methods for more detailed description of the process). Code was written in Mathematica 12 (Wolfram Research, see Supplementary Information).

The existence of life-history ‘lottery winners’ is apparent in all model conditions, but the maximum age reached increases dramatically as mortality rate declines below 2% (Fig. 1a), with a doubling

of maximum age between 1% and 0.5% mortality, and substantially but less dramatically with population size. The range of mortality rates that most profoundly affects tree longevity corresponds directly to empirical values estimated from global forests, indicating that small increases in forest mortality can have a dramatic impact on the potential age of trees in that population. Additionally, while maximum age does increase with population size, this effect is most dramatic among smaller populations, indicating the sensitivity of trees in small fragmented forests to this process.

Our models also provide an objective estimate of the time required for a forest to reach climax age, following the establishment of an even-aged cohort of mature trees. Forests established after catastrophic fire, storm or anthropogenic conversion by either managed restoration or natural regeneration would resemble the initial conditions of our model. The climax age of a forest is a linear relationship between $\log(\text{population size})$ and mortality rate (Fig. 1b), taking several centuries given intermediate population sizes and mortality rates below 2%. We define this climax age as the point where the age structure of the population stabilizes (Supplementary Fig. 1) and the forest becomes older than the oldest surviving individual. This moment in forest regeneration also corresponds closely to when the oldest individual becomes the lone representative of its age. These patterns are relevant to most modern forests, particularly in the northern temperate regions, where even-aged stands have regrown in abandoned agricultural lands²³. Given prevalent natural mortality rates, the climax status of the forest remains centuries in the future. With increased mortality rates observed in forests around the world^{24,25}, the potential for the emergent ancient age groups may become impossible.

To understand the contribution of different apparent groups in the population, we objectively defined thresholds for three age classes (mature, old and ancient) based on the properties of the rank–age distribution of the populations, after the population had reached climax age (Supplementary Fig. 2). The general properties of mature and old age groups remain relatively consistent across model conditions (Fig. 2). Mean age in the entire population does not respond to population size but does respond in a linear fashion to mortality rate, being only 14 years (plus the average age to attain the established mature stage) at 5% mortality and 69 years at 1% mortality, a fivefold change in both values (Figs. 2 and 3). The time to establishment needs to be added to these ages, and many trees can spend decades in the sapling stage. The proportion of old trees in the population (~24.4%) remains constant across all model conditions, while the proportion of ancients remains constant for a particular mortality rate (for example, ~1% of population for 1.5% mortality) but increases with declining mortality (for example, ~1.5% of population for 1% mortality compared with 0.2% of population for 5% mortality).

The ancient trees, particularly the oldest, display the greatest degree of responsiveness to changing model conditions. Some individuals obtain truly astonishing ages in relation to the mean age of the population, which, as noted above, is already substantially greater than the median population age and even the median oldest individual across replicates (Fig. 3; see full range of variation in Supplementary Fig. 3). Even in the smallest populations, individuals achieve ages that are significantly more than the mean maximum age, and the frequency and magnitude of these outliers increase with declining mortality (Fig. 3). Essentially, a life-history ‘lottery winner’ can emerge at any timepoint. The maximum age obtained by these lottery winners is substantially greater than even forest climax age, indicating that, even after population age structure has stabilized, the ancient trees continue to become more unusual and idiosyncratic for many more centuries. Unfortunately, the ancient age group that emerges from a stochastic death process, and thus their impact on evolutionary dynamics, can only be found in old-growth forests. Anthropogenic forest conversion resets the clock on this long emergent process.

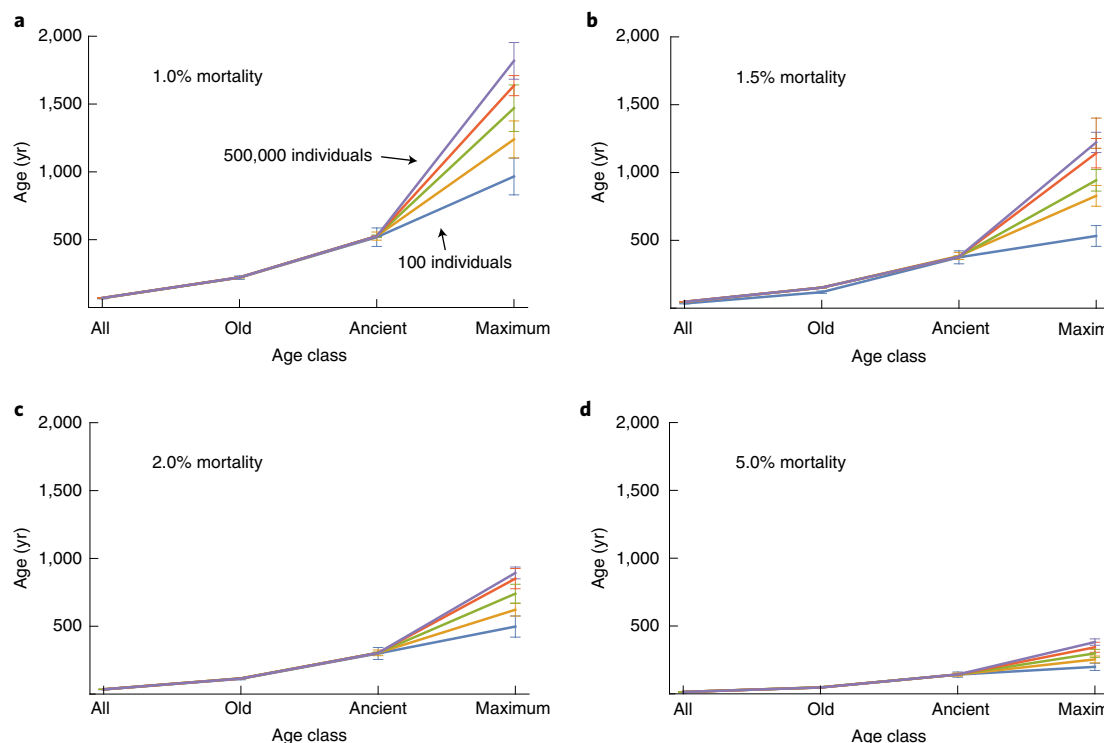


Fig. 2 | Mean age and standard deviation of three age classes, given different mortality rates and population sizes, across 25 replicates. a–d, Age distribution of age classes at mortality rates of 1.0% (a) 1.5% (b), 2.0% (c) and 5.0% (d). The lines connect results given different population sizes: 100, 1,000, 10,000, 100,000 and 500,000 individuals, from bottom to top.

Vital evolutionary resource over long periods of time

Environmental conditions change on many different timescales and are an emergent selective force composed of numerous factors. To explore the impact of the demographic patterns we observed on population-level diversity, we constructed a scenario of millennial environmental change, where fitness is determined by four different underlying regular cycles (Fig. 4 and Supplementary Fig. 4). Given a mortality rate of 1.5% and the assumption that trees become established (and thus mature trees and part of our model simulations) under environmental conditions for which they are most fit, fitness diversity in each of the three age classes varies with increasing population size in different ways. Compared with the overall distribution of fitness values present in the environment over 1,000 years, the mature individuals correspond closely with current environmental conditions but poorly with fitness averaged over the entire time period. This distribution for mature individuals does not change with population size because this age class is present and consistent in all populations. The old trees, in this particular model run, closely match fitness diversity in the mature group at the smallest population size (Fig. 4), but this result varies considerably given different sampling points. Fitness diversity among ancient trees continues to shift with each change in population size. At the smallest population size, ancient individuals are largely absent, and as they appear, initially, they are substantially different from either of the two age groups and current environmental conditions. With increasing population size and a corresponding increase in abundance and age of ancient individuals, the ancient fitness diversity begins to converge on the distribution of overall environmental variation (Fig. 4e). These two groups (mature + old and ancient) essentially bracket historical environmental change on either side.

The environmental scenario discussed here represents a single example for the scale and frequency of environmental change and the chosen sampling time. These results represent only a

case study but, fundamentally, closely correspond to our ability to study forests, given project timescales of at most several decades and generally much less, while the interaction between demographic dynamics and environmental change clearly plays out over many centuries. First, perhaps the clearest lesson to be drawn from our results is the limited power of any current study, which represents a single snapshot in time. Additionally, mature trees, the youngest age class, are present and predictable in all populations, no matter the model parameters, although median age does decline linearly with increasing mortality rate. These mature individuals are constrained to environmental conditions experienced in the recent past. Second, old trees are also present and consistent in all but the smallest populations and generally reflect the central tendency of environmental history, particularly if the timescale of change and the mean age of old trees roughly correspond. Third, the ancient trees in intermediate-sized populations can poorly fit current environmental variation but represent a complementary range of diversity compared to the other age groups. Finally, because each ancient tree can differ in age from other ancient trees by decades and even centuries, every individual represents a unique set of environmental conditions that existed when they established.

These ancient trees can be a very valuable resource for the population, if temporal scales of environmental variation extend beyond the age of even old trees, thus bridging between extreme and infrequent environmental conditions that the population might not survive without the ancient trees. Conversely, these ancient trees might harbour traits and genes that are poorly fit to current and more short-termed environmental change and that, if they dominated reproduction, could reduce population fitness. If environmental changes were directional, moving steadily away from any central tendency, these ancient trees can present a disadvantageous anchor on change in the population. Ultimately, many other

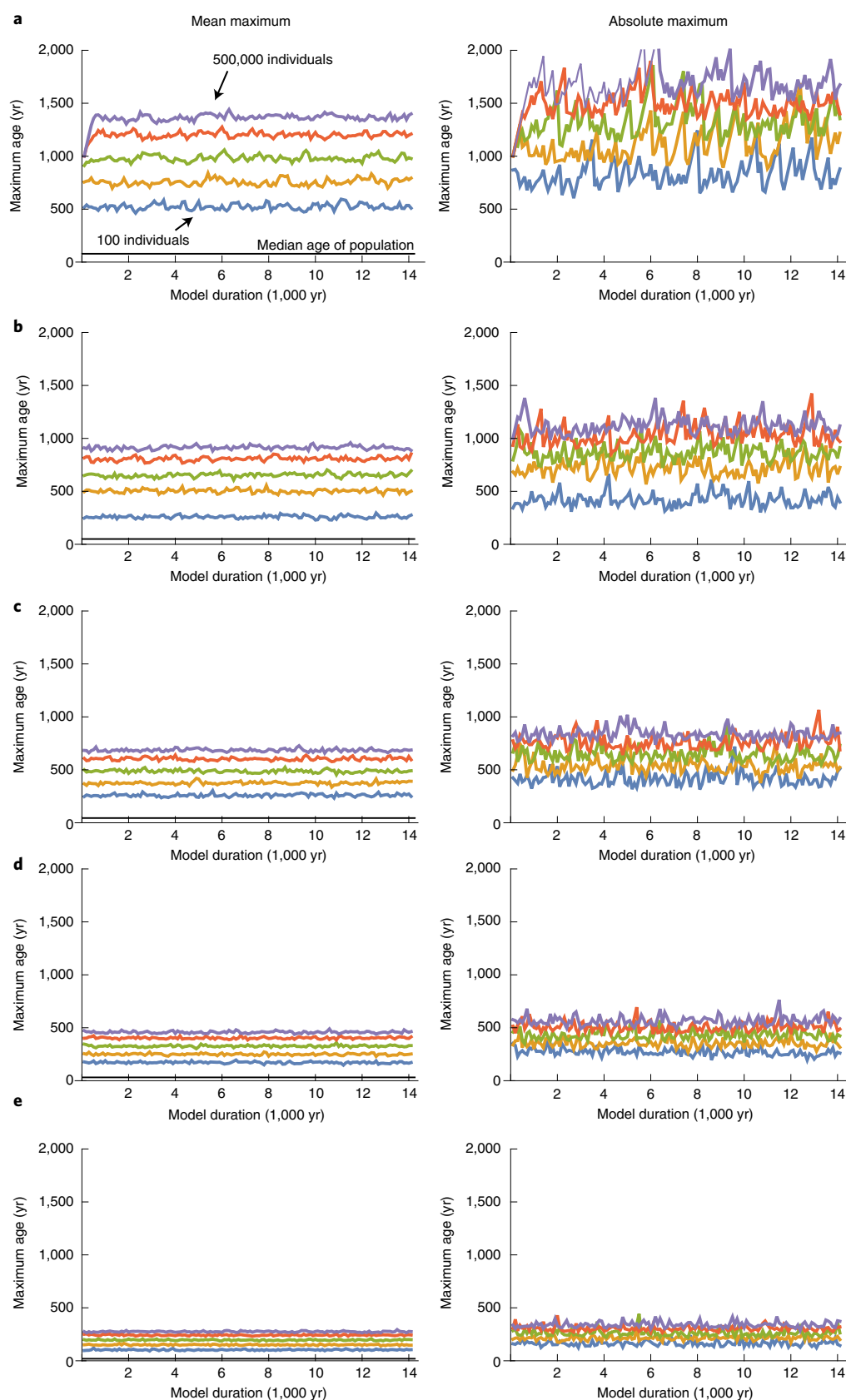


Fig. 3 | Mean and absolute maximum age achieved across 25 replicates over 15,000 years, given different population sizes and annual mortality.

a–e, In each panel, time is shown on the x axis, running from 1,000 to 15,000 years, and maximum age is shown on the y axis. Solid coloured lines illustrate population sizes: 100, 1,000, 10,000, 100,000 and 500,000 individuals, from bottom to top. Annual mortality rates are shown in each row: 1.0% (**a**), 1.5% (**b**), 2.0% (**c**), 3.0% (**d**) and 5.0% (**e**). Mean maximum age across replicates is shown in the left column and absolute maximum age is shown in the right column. Overall median age of the entire population, which was the same for all population sizes, is shown by the solid black line in the left column.

possible environmental dynamics should be explored, particularly if environmental change is directional and not constrained to a central value. The rarity and difficult identification of ancient trees makes their discovery and direct study nearly impossible using traditional ecological sampling methods. Instead, the disproportionate and profound impact these ancient trees have on the adaptiveness and sustainability of the population and species requires an innovative and specialized modelling approach. A full exploration of these dynamics requires a comprehensive analytical approach to summarize results across a range of environmental conditions to obtain the general properties of this dynamic.

Variance in generation time

To assess the evolutionary buffering capacity of the emerging age class structure in these populations, we examined variation in three estimators of generation time, given different population sizes and mortality rates. The first estimator assumes that all individuals alive in the population have an equal probability of producing successful offspring. The second estimator assumes that older individuals contribute disproportionately to the next generation, based on their age and not the number of individuals of that age. The third estimator assumes that only the oldest individual alive produces offspring. The first two estimators are basic methods of estimating generation time, while the last value calculates maximum possible generation time in a population over a given period of time.

The generation time for all three estimators increased with decreasing mortality rate, with only slight changes in the first estimator but a roughly sixfold increase for the last estimator (Table 1). These values also changed dramatically with increasing population size, increasing two- to threefold within each mortality rate. The first and third estimators essentially represent the lower and upper bounds for generation time in the population. Given that selective environments change through a complex cyclical process of several underlying patterns, extreme environmental conditions can return over time periods of decades or hundreds of years (Fig. 4a). The greater longevity of ancient trees increasingly bridges the temporal gap between the return of these environmental extremes (Fig. 4b–e). If individuals that establish during those extreme periods are more fit for these conditions, they can produce offspring that are likely to have advantageous alleles that facilitate establishment during those extreme conditions. As fecundity is generally maintained in ancient trees²⁶, their contribution to regeneration during these extreme but rare climatic conditions can be disproportionate. Overall, despite the rarity of the ancient individuals, each ancient individual is connected to a unique historical circumstance (Fig. 4). They create a rich and deep genetic diversity within the community that can bridge the gaps between rare and extraordinary environmental conditions. In particular, given predictions of global climate change, the baseline itself of cyclical environmental change is shifting and the amplitude of change is increasing, driving conditions towards more and more extreme values, further accentuating the importance of these ancient reservoirs of valuable adaptive capacity at the outer margins of genetic diversity.

Mechanisms to deal with ageing in ancient trees

Several mechanisms have evolved in individual trees to enable extreme longevity and deal with negative effects of ageing (Fig. 5). In general, they can be grouped into two non-mutually exclusive categories: senescence avoidance and ageing tolerance. Senescence avoidance includes either escaping from or preventing senescence. Clonality in plants allows resetting the clock and escaping the wear and tear of ageing²⁷. Although clonality is tightly linked to long lifespans, it only relates to the genotype, not the individual^{3,28,29}. More relevant to the model presented here, ancient, non-clonal trees usually show another mechanism to prevent senescence for a very significant part of their lifespan. Growth and senescence are two essential parts of the same coin. While plants are growing, they cannot senesce. Senescence implies a reduction in vigour; therefore, continuous growth is the most effective mechanism to prevent senescence. Several long-lived plant species follow this strategy, including redwoods (*Sequoia sempervirens*), which attain their maximum height at relatively advanced ages and generally do not show a decline in vegetative growth vigour with increasing age³⁰. This strategy has, however, its limits. Due to functional leaf characteristics in redwoods, increasing leaf water stress due to hydraulic and mechanical constraints may ultimately limit leaf expansion and photosynthesis, thereby preventing further height growth beyond 130m even with ample soil moisture³¹. But trees have evolved strategies to prevent death from water stress once maximum height has been reached.

Stress tolerance is indeed a mechanism of ageing tolerance, since it serves to delay death as trees age. In ancient trees, the ability to maintain pluripotent meristems is key for resistance (growth memory), resilience and stability of populations^{32,33}. While shoot apical meristems lead directly to vegetative and reproductive growth, axillary meristems are particularly important for plant branching and regeneration after damage³⁴. Ancient trees possess huge vegetative plasticity, even through epicormic shoots in consequence of severe disturbances³ (Fig. 6a). In fact, the modular tree growth form, through both shoot apical meristems and axillary meristems aboveground and root apical meristem and lateral meristem belowground, creates a colony of competing genotypes that vary in their genotypic and phenotypic fitness according to their historical development. The cambial meristem continually renews the vascular system of the tree, responding to local conditions, both temporally and spatially, essentially creating a record of change and resilience in the tree wood. Meristematic tissues, both pluripotent and constantly renewing themselves, enable the tree to essentially be potentially immortal^{28,29}. This pluripotency is also observed in our ability to propagate scion wood from old trees, which is often rejuvenated to some extent when grafted onto a younger tree, truly enabling the possibility of potential immortality for a particular genotype. Ultimately, although somatic mutations can accumulate to some extent, intra-organismal genetic heterogeneity can be selected for and provides direct fitness benefits against short-lived pests and pathogens^{35,36}. Epigenetic imprinting^{37–39} across their canopies over centuries also allows them to be particularly good at tolerating stress and preventing the wear and tear of ageing and passing on advantageous traits and phenotypes.

Fig. 4 | Population demographics in relation to changing environmental selection pressure (Supplementary Fig. 4), given an annual mortality rate of 1.5%. a–e. Each panel illustrates the population of living individuals, as horizontal lines, observed at a single sampling time (left column) and the distribution of population fitness values at the time of establishment for three age classes of trees (right column). Each row of graphs corresponds to a different population size: 100 (a), 1,000 (b), 10,000 (c), 100,000 (d) and 500,000 (e). Lines are colour-coded according to age class: blue, mature; red, old; black, ancients (see Methods for technical definitions). In the left column, individual trees are represented by a horizontal line, originating at the time of their establishment to the sampling time. The emergent environmental fitness value (y axis) is shown by the red waveform, which is the summative outcome of four underlying cycles (Supplementary Information 3) changing over time (x axis). In the right column, the distribution of age class fitness is shown. The error bars illustrate the 25% quantile of population fitness, and the diamond corresponds to population median. The first thin black error bars with the white diamond illustrate the observed environmental fitness value over the 1,000-year period, including the horizontal black line, which corresponds to the mean environmental fitness value over this time period.

Living stores of past selection and future adaptive capacity

Abundant evidence suggests that trees can obtain extreme ages, well over a millennium, due to their unique modular growth form

and physiological plasticity and that they regularly achieve ages of many centuries. Old-growth forests are generally characterized by an overall spatially random mortality^{40,41}. A stochastic model

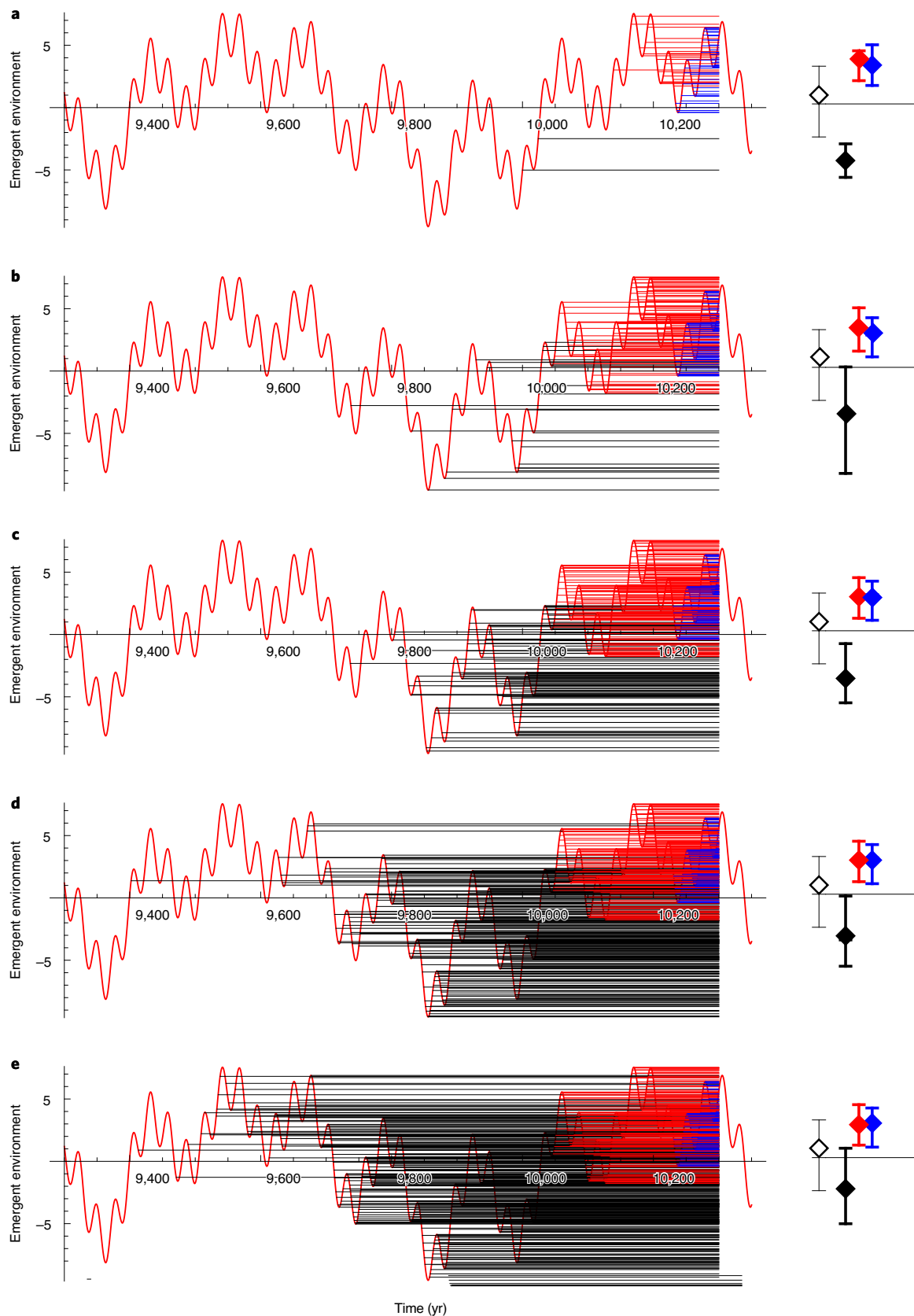
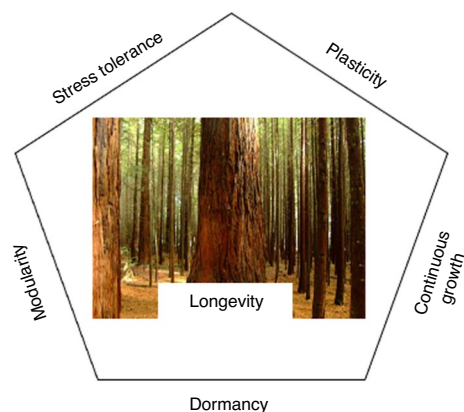


Table 1 | Variation in estimated generation time, given different community sizes (rows) and mortality rates (columns)

	1.0%			1.5%			2.0%			5.0%		
	1	2	3	1	2	3	1	2	3	1	2	3
100	121	121	449	102	103	206	102	103	207	<100	<100	<100
1,000	121	159	649	106	125	432	102	111	319	<100	<100	105
10,000	121	239	822	106	174	563	102	140	415	<100	100	136
100,000	121	341	992	106	232	689	102	184	515	<100	103	198
500,000	121	403	1121	106	281	776	102	218	588	<100	108	213

The values for each combination of parameters illustrate mean generation time assuming contribution to the next generation is (1) equal among all individuals; (2) proportional to age class; and (3) only by the oldest individual. 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. As the temporal resolution of the analysis is in 100-year steps, the lowest value for generation time is 100 years.

**Fig. 5 | Major mechanisms evolved by ancient trees to defy ageing.**

Lack of programmed senescence enables very long lifespans in trees and implies that death is largely due to stochastic events. The indeterminate lifespan of trees arises from a combination of mechanisms that serve both to prevent senescence (modularity, continuous growth, dormancy) and tolerate ageing (stress tolerance), creating enormous potential and flexibility in longevity.

investigates the theoretical relationship between average mortality and age structure in old-growth forests assuming an average mortality rate that depends on species (that controls longevity traits and mechanisms) and local environment (soil, climate, disturbance regime). Model output agrees with real data, even in the case of long-lived tree species such as *Juniperus* spp., *Pinus aristata/longaeva* in arid subalpine environment (strip bark trees of stress tolerant species) or *Sequoia sempervirens* (fire-resistant species with canopy rejuvenation ability). Being characterized by very low mortality rates (less than 0.005 (ref. 42)), these conifers can attain more than two millennia of age¹², confirming the maximum ages calculated by the stochastic model (Supplementary Information 2). Such extreme longevities are realized because these species maintain the tree habit compartmentalizing and repairing their canopy in consequence to disturbances owing to specialized traits such as wood durability, strip bark behaviour (juniper and pine, modularity) and canopy rejuvenation (*Sequoia*). Temperate broad-leaved trees, such as *Fagus sylvatica* or *Quercus petraea*, being characterized by a much higher mortality rate (for example, 0.015–0.02 (ref. 41,42)), attain maximum ages between 600 and 900 years^{43,44} (Fig. 1), indicating that ancient trees are lottery winners, with the chances of winning varying on the basis of the species and the environment. However, future studies should consider the comparison of model output with real mortality and age data collected in the same old-growth forests comparing population demographics and fitness also in relation to

the role of biotic versus abiotic disturbances/fluctuations. Finally, given the trend of increase in mortality that seems to characterize the last decades in certain environments (for example, western United States⁴²), the proposed model can provide demographic data to evaluate the impact of global changes on the carbon cycle⁴⁵ and the conservation of biodiversity⁴.

Critically, in regenerating forests or populations of very small size, the long demographic tail of ancient trees is missing. Our results suggest that climax forest containing ancient trees obviously requires several centuries, even when mortality rates are relatively high (3%). Estimates that old-growth forest can be achieved in 150 years (ref. 46) neglects the impact of ancient trees. These ancient trees are indicators of the degree of development in old-growth processes⁴⁷. Old and ancient trees are unique proxies for reconstructing past climate and environment⁴⁸. Such old trees have survived multiple decadal (Atlantic Multidecadal Oscillation and Pacific Decadal Oscillation generally lasting between 30 and 70 years) and even longer contrasting climatic phases (Medieval Warm Period, Little Ice Age, global warming). While our model assumes neutrality, the survivorship of some trees also indicates the growth conditions where functional traits⁴⁹ confer resistance to biotic and abiotic stresses. If the trend of increasing mortality persists in the coming decades²⁵, thousand-year-old trees will become a very rare phenomenon in the primeval landscapes and when the mortality trend reverses, their recovering will take a very long time (centuries or even millennia).

Finally, ancient trees represent a major reservoir for deep genetic diversity that can bridge long temporal gaps between extreme environmental conditions. While these ancient individuals are rare in the population, their existence can have profound impacts on population evolutionary dynamics, particularly regarding coalescent and lineage sorting processes, which are both defined by generation time^{50,51}. Given our poor understanding of demographics or population dynamics in forest trees, the impact of possible variation in generation time, caused by skewed or unusual demographic structures^{52–54}, is not frequently considered. We demonstrate that the presence of ancient trees in the community greatly increases the variance in generation, extending and increasing the variance in coalescent times and lineage sorting processes. While evidence of senescence, through diminished seed output, has been recently reported²⁶, older trees often do contribute a disproportionate number of seeds during a fruiting event⁵⁵. While seed production does senesce with age²⁶, no evidence exists in regard to senescence in pollen contribution. Older trees' participation in population genetics of the community remains significant (Fig. 6b), despite their rarity in the community. Empirically, tree genomes are often noted for their high levels of heterozygosity and typically exhibit higher within-population levels of genetic diversity compared with between-population levels, supporting this hypothesis. This suspended process of coalescence would also address the paradox of fast microevolution but slow macroevolution⁵⁵.



Fig. 6 | Canopy rejuvenation and seed production in old trees. a, Epicormic branching after a severe crown disturbance in an old sessile oak. **b,** Acorn production in 600-year-old sessile oak trees in the Aspromonte National Park where the oldest dated temperate flowering tree in the world (930 years) is still fruiting¹².

For all of these reasons, old-growth forests with their unique stock of ancient trees are becoming increasingly important to protect. Losing these trees is like species extinction, in that an irreplaceable genetic resource is being lost. Ecologically, ancient trees are known to be unique biodiversity hubs⁵⁶ that provide key or unique ecosystem functions unparalleled by managed forests. They contribute disproportionately to the forest rate of carbon sequestration, as this rate continuously increases with tree size⁵⁷. But these ancient trees, perhaps most critically, are an irreplaceable evolutionary resource for the tree species themselves. The loss of these ancient trees can greatly reduce the evolutionary potential of the species. Preserving and restoring ancient trees everywhere in the world, from the heart of old-growth forests to tiny fragments in managed forest or along roadsides, is an urgent goal for a sustainable future. We strongly advocate research focused on these ancient trees and their contribution to the future adaptive capacity of our global forests.

Methods

Simulation model. A simple technique for imposing a stochastic mortality rate on a population of individuals with a constant number of individuals in the population was written in Mathematica 12 for Mac OS (Wolfram Research). The simulation involves no spatial or fitness component into the likelihood of death, but instead all individuals are equally likely to perish. The initial settings mimic recovery of a site after a complete conversion, with all individuals starting at the same time and same age. All individuals are considered established once they appear in the population simulation with equal probability of mortality.

Each step in the simulation is equivalent to a year, and the dead individuals are chosen randomly and then removed from the population, with the number of individuals to be removed being the annual mortality rate multiplied by the population size. Surviving individuals have a year added to their age and a new cohort of 1-year-old individuals replace the dead individuals removed from the population. This step is repeated for the duration of the simulation model. All models were run for an equivalent of 15,000 years.

The parameters explored in the model vary by population size (100, 1,000, 10,000, 100,000 and 500,000 individuals) and annual stochastic mortality rate (0.001, 0.005, 0.01, 0.015, 0.02, 0.03 and 0.05). Each set of parameters was examined across 25 replicates. To explore the impact of increasing population size, one set of replicates was also run for one million individuals given a mortality rate of 0.015. Little variation was observed in the results, and further exploration of a broader parameter space did not seem warranted. The mortality rate of 0.02 appears to be a bit of a threshold as the results change quickly below this rate, but the lower bound of mortality studied here (0.001) does not appear biologically

relevant as the results do not reflect empirical evidence from global forests or other organisms that match this mortality model. More detailed exploration of the impact of small population sizes on these dynamics is warranted, as the lower bound of 100 individuals generated unusual results and presented certain challenges to the model effort.

To simplify the analysis of the demographic patterns, samples were taken of the population every 100 years during the 15,000-year time period and individuals were grouped by age class. All subsequent analyses were performed on these demographic tables. Given the initial conditions of the model, where an even-aged cohort of individuals dominate the population in the beginning of the model but slowly go through attrition until the youngest age class becomes the most abundant, we determined that this point where the age class structure becomes stable represents the population climax age, at which the impact of the reset no longer has an effect. Population climax age was technically defined as the point at which the oldest age class is represented by a single individual. These dynamics are explained in greater detail in Supplementary Information 1. All analyses were performed after the demographic patterns became stable.

Age group classification. We detected an emerging group of individuals in our simulations that were substantially older than the rest of the population. We deemed these individuals as ‘ancient’ and described them as life-history lottery winners because they were always a small fraction of the overall population but departed entirely from the population characteristics, extending a very long and thin tail to the distribution of ages (Supplementary Fig. 2). Further exploration of the age–rank distribution revealed that three separate segments of the population (mature, old and ancients) could be identified objectively by age, corresponding to the different parts of the age–rank curve. The threshold for old trees could be efficiently determined as twice the age of the median age of the entire population. Mature trees are simply those trees younger than this threshold. This threshold, easily calculated, corresponds closely to the inflection point in the rank–age distribution where the steady and linear progression becomes nonlinear (Supplementary Fig. 2). The threshold age between old trees and ancient trees was technically defined as the point where the subset of five consecutive ages present in the population are separated by an average of 2 years, that is, the span of time encompassing the next five oldest trees equals an 8-year spread. We found that applying this rule to different population sizes resulted in different threshold ages for ancients, which increased with population size, but the absolute number of individuals above this threshold remained constant across population sizes. However, plotting this threshold on the rank–age distributions revealed that it did not correspond well with the properties of the curve and only included a very small portion of the obvious long tail of very old individuals. Instead, we found that the 10,000 individual population appears to represent a point at which the dynamics become predictable at larger population sizes. Setting the threshold for ancient age as the point where the rule was accepted for 10,000 for all population sizes then fit the properties of the curve.

Exploring environmental fitness dynamics. To explore the role of individual trees in these different age groups given cyclical environmental change, we simulated an environmental fitness value that is the summation of four different cycles that recur over the time period of the simulation. Because of the large possible parameter space given this type of model, we wrote a 'tunable' but arbitrary equation that generated an emergent pattern that was appropriate to empirical patterns of environmental cycles that occur on various temporal scales, from decades to millennia. The equation is the summation of

$$4(\sin[x \times 0.01]) + \sin[x \times \text{wave1freq}] + \text{wave2amp} \times \sin[x \times \text{wave2freq}] + \text{wave3amp} \times \cos[x/\text{wave3freq}];$$

where x is time and the variables $\text{wave\#amp}$ and $\text{wave\#freq}$ correspond to the properties of the specific environmental cycle. These variables could be easily modified, and a representative set was chosen to examine the impact of the different age groups over these fitness cycles. See Supplementary Information 3 for a detailed description of the process and the background for the background environmental fitness value used in Fig. 3.

To assess the impact of the different age groups on the adaptive capacity of the population, we assumed that fitness determined the ability of the individual to establish. Therefore, the individuals were assigned the fitness value present in the environment at the time of its establishment. For illustrative purposes, a single sample point was chosen arbitrarily for a single replicate (year 10,300 in the tenth replicate) to examine the distribution of fitness values for each age group. We feel this approach is adequate and corresponds to our ability to collect empirical data on these types of long-lived individuals, which is inherently latitudinal and not longitudinal in quality. Additionally, this type of analysis is novel and protocols for exploring the properties of population fitness would require the development of a new set of tools. This future work would be required to comprehensively explore the full impact of different age groups across all environmental situations, but we feel that this effort is beyond the scope of the current analysis.

The population descriptors of fitness for each age group were compared with the overall background fitness value over 1,000 years, across population sizes and mortality rates.

Estimation of generation time. Generation time was estimated in three ways: (1) all living individuals in a cohort have equal probability of contributing an offspring to the establishing cohort, regardless of their age; (2) individuals in each age class have the same probability of contributing an offspring to the establishing cohort, regardless of their abundance; and (3) only the oldest living individual contributes to the establishing cohort. These three estimators were calculated (1) by randomly choosing an individual from the last living cohort produced at the end of a simulation, which served as the 'tip' individual; (2) the time of establishment for the tip individual was determined by subtracting the individual's age from the time of sampling in the simulation; (3) the progenitor of the individual is selected on the basis of the three criteria described above: (1) randomly among all living individuals; (2) randomly among all age classes present; and (3) the oldest living individual. Steps 2 and 3 were repeated until the beginning of the simulation was reached, keeping track of the number of individuals required to traverse the entire simulation, from the end to the beginning. Generation time was then calculated by dividing the length of the simulation (15,000 years) by the number of individuals required to span from beginning to end. This entire process was repeated ten times for each of the 25 replicates, meaning that a total of 250 estimates for generation time were calculated for each combination of model parameters.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data used in the analyses were generated from the code provided. The authors strongly recommend that the data be generated directly from the code to demonstrate the reliability of the methods and to verify that the results are the same in different computing environments and settings. Computation time to generate the dataset was less than 8 h on a MacBook Pro with 2.5 Ghz Dual-Core Intel Core i7 processor and 16 GB of RAM. The original dataset used in this publication is available upon request from the corresponding author.

Code availability

The models and analyses were written in the Mathematica 12 programming environment. A notebook containing the simulation model and the code used to produce the results and figures has been uploaded to the publication website. Code can also be provided upon request by the corresponding author.

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Author contributions

C.H.C. and S.M.-B. conceived the idea. C.H.C. conceived of and wrote the simulation models, performed the analysis and wrote the manuscript. G.P. and S.M.-B. helped improve the analysis and wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Research sample	The research was conducted entirely through computer simulations. Twenty-five replicates were generated for each combination of study parameters, which included 100, 1000, 10000, 100000, and 500000 individuals in the population and 0.5, 1.0, 1.5, 2.0, 3.0, and 5.0% annual mortality.
Sampling strategy	The age of all individuals existing in the population were sampled every century over 15,000 'years'.
Data collection	The age of all 'living' individuals in the populations were sampled each century over the course of the 15,000 year simulation.
Timing and spatial scale	No spatial parameters were used as we focused on exploring the properties of neutral selection conditions and the effects of a stochastic mortality rate. We imposed an annual death rate, with a randomly selected number of individuals, corresponding to the mortality rate, experiencing death while the same number of corresponding individuals were introduced into the community. Therefore the community size was steady state, for simplicity sake.
Data exclusions	No data was excluded.
Reproducibility	Twenty-five replicates were performed for each combination of model parameters. Comparable results were generated using a different coding technique for imposing a stochastic mortality rate on a population of individuals.
Randomization	All individuals in the population experienced identical mortality rates within each set of replicates for a particular mortality rate.
Blinding	No blinding was necessary because the simulation produces the results from all combinations for all 25 replicates simultaneously and the analyses were conducted identically across all data. Samples were all treated identically.
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