Loss of Earth's old, wise, and large animals

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Earth's old animals are in decline. Despite this, emerging research is revealing the vital contributions of older individuals to cultural transmission, population dynamics, and ecosystem processes and services. Often the largest and most experienced, old individuals are most valued by humans and make important contributions to reproduction, information acquisition and cultural transmission, trophic dynamics, and resistance and resilience to natural and anthropogenic disturbance. These observations contrast with the senescence-focused paradigm of old age that has dominated the literature for over a century yet are consistent with findings from behavioral ecology and life-history theory. Here, we review why the global loss of old individuals can be particularly detrimental to long-lived animals with indeterminate growth, increasing reproductive output with age, and those dependent on migration, sociality and cultural transmission for survival. Longevity conservation is needed to protect the important ecological roles an ecosystem services provided by old animals.

REVIEWS

Aging is a fundamental process that has long been the subject of philosophical and scientific interest (Box 1). While the neg-ative aspects of aging have been the focus of extensive litera-ture, the ecological and conservation importance of old individual animals in the wild is gaining recognition. Old age-classes of many animal populations have declined or been eliminated due to human impacts. Across five ocean areas, the oldest age-classes of fish have been depleted in 79–97% of populations (*1*), extremely old corals are being harvested but are effectively irreplaceable within human lifespans (*2*), and other aquatic fauna (*3*, *4*) have diminished size and age-struc-ture in response to past and on-going impacts. On land, poaching, trophy hunting, predator culling, and recreational harvest often target the largest animals based on desirable traits, such as large antlers, horns and tusks (*5*), commonly leading to a younger, female-biased age-structure with im-pacts on recruitment and destabilized social structure (*6*). Coupled with direct impacts of harvest, other anthropogenic pressures, including habitat loss, disease, extreme climate events and river regulation, can exacerbate losses of large and old individuals (*7*–*11*).

The gradual loss of human knowledge about the historical conditions of animal populations and ecosystems defines the shifting baseline syndrome (*12*). Many people remain igno-rant of the historically higher abundance of large, old animals (Fig. 1), and are therefore ignorant of their ecological and conservation importance. Human impacts that reduce the abundance of old animals has been shown to affect popula-tion and ecological dynamics (*6*, *13*–*15*). Certain functions of old individuals (e.g., reproductive, trophic, knowledge, wisdom, and leadership; reviewed below) cannot be replaced by younger adults. The ecological and conservation im-portance of old animals has parallels to that of old-growth trees (*16*, *17*)—older and larger individuals are economically valuable and vulnerable to overharvesting (*1*, *18*), often have greater reproductive output and contribute disproportion-ately to recruitment (*19*, *20*), have unique responses to cli-mate change (*21*), and sometimes provide critical habitat structure (i.e., deep ocean coral and Antarctic sponges (*22*); Fig.

1A). Loss of old trees and animals reduces demographic buffering and storage effects that can stabilize populations in fluctuating or perturbed environments (*15*, *23*, *24*).

While the ecological and conservation importance of old trees (*16*, *17*), megafauna (*10*, *25*), and reproductive values of big, old fish within exploited stocks (*26*) has been reviewed previously, our objective is to synthesize the ecology and con-servation of old individuals across a spectrum of animal taxa (Fig. 2). Since the negative aspects of biological aging have been widely documented, our narrative review is focused on understanding the benefits of old age in animals. Here we highlight new directions for research, policy and planning. First, we review the old animal storage effect and long-lived life-histories as fundamental concepts to understand the ben-efits of old individuals, and how their loss affects species dif-ferently. In reviewing the contributions of old individuals and storage effects we include: i) reproduction and recruitment; ii) behavior, knowledge, sociality and culture; iii) ecosystem structure and function; and iv) resistance and resilience to global change (Fig. 2). We conclude by discussing longevity conservation as a solution, calling for a fundamental shift in

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Advantages of a long life and the old animal storage ef-fect

Compared to short-lived animals, long-lived species tend to exhibit more stable populations (*27*) with higher standing bi-omass of adults in middle and old age classes–the embodi-ment of what has been termed the “old animal storage effect” (Fig. 3). Storage effects can take several forms, including egg banks or adults of long-lived species that buffer populations during recruitment failure and persist despite adverse or fluc-tuating environmental conditions (*23*, *24*, *28*). The long-term accumulation of older adults and their more stable biomass contributes to advantageous storage effects associated with reproduction and recruitment, behavior, knowledge, sociality and culture, ecosystem structure and function, and resistance and resilience to global change reviewed below. Larger spe-cies and larger individuals within populations are often able to monopolize resources (*29*), but their populations are prone to extinction due to low intrinsic rates of increase (rmax) and demographic resilience (*30*). Whether or not the storage ef-fect explains species coexistence remains an active area of re-search (*31*), but here we focus on the importance of older individuals to the ecology and conservation of long-lived spe-cies.

Long lifespans–usually associated with large body size, slow growth, late maturation, and low adult natural mortal-ity–have evolved in all vertebrate classes and in many inver-tebrates. In general (Fig. 3), long-lived species are relative equilibrium (i.e., *K*-selected) or periodic (bet-hedging) life-history strategists as opposed to small, short-lived opportun-istic (*r*-selected) strategists (*32*, *33*). Young and old individu-als exist in all species, but longevity varies greatly. Maximum known longevity in vertebrates ranges from approximately 59 days in the pygmy goby (*Pandaka pygmaea*) to at least 392 years in the Greenland shark (*Somniosus microcephalus*), and the lifespan of invertebrates ranges from less than 24 hours to 10,000 years and beyond in some sponges (Fig. 1A) (*34*, *35*).

We hypothesize that reduced abundance of old individu-als disproportionately impacts the storage effects of long-lived species closest to the periodic and equilibrium life-his-tory endpoints of a triangular continuum (Fig. 3), because these species have evolved strategies that rely on high adult survivorship and long life expectancy to maximize fitness in response to specific environmental challenges and opportu-nities (*27*, *33*). Having evolved strategies to cope with high natural adult mortality, short-lived opportunistic (*r*-selected) species are expected to be less vulnerable to losses of older adults. More research is needed to examine the degree to which species having different trait combinations within the life history continuum are vulnerable to population decline when there is loss of old individuals (Box 2).

Patterns of age-related biological decline appear inde-pendent of lifespan across diverse taxa (*36*). However, many long-lived species with indeterminate growth have long post-maturity lifespans, low adult mortality and increasing repro-ductive output with body size (see Reproduction and Recruit-ment). This is just one combination of traits which can lead to negligible or negative senescence, whereby certain biolog-ical functions increase with age (*37*). There appears to be a phylogenetic effect whereby large, long-lived fishes and other periodic ectotherms with indeterminate growth generally have greater reproductive output with age (see Reproduction and Recruitment). In contrast, long-lived endotherms with determinate growth, including some large mammals and other equilibrium life-history strategists, exhibit senescence in terms of reproductive output, but often acquire greater knowledge and enhanced behavioral responses (see Behavior, Knowledge, Sociality and Culture) that facilitate survival of offspring and other related individuals (Fig. 3). Yet what remains to be determined is whether disproportionately influ-ential functions of old individuals only apply to certain species or are common and relate generally to life-history strategies as we hypothesize (Box 2).

An old-animal storage effect of periodic strategists (e.g., tuna, giant clam, sea turtles; Fig. 3) is achieved by delayed maturation, sometimes for decades, until attainment of suffi-ciently large body size and energy/nutrient stores to produce large batches of small offspring/propagules that disperse into the environment with minimal or no parental care (*33*). By virtue of their high investment in somatic growth, which is often indeterminate, adult periodic strategists typically are large-bodied and long-lived. Owing to demographic buffering (Fig. 3), adult age-classes of long-lived periodic and equilib-rium strategists are expected to be resistant to environmental variability (*28*, *38*), such as seasonal changes in temperature, precipitation, or hydrology. In the absence of anthropogenic pressures, this resistance contributed to historically large standing biomass of old and large fish and wildlife (*3*, *39*).

Old adults of many periodic animals are migratory, trav-eling long distances to feed or reproduce (*13*, *20*), and the small offspring of these animals have high rates of natural mortality and fairly passive dispersal facilitated by wind or water (*40*). Even though recruitment variation is high in periodic strategists (*13*, *40*), their long lifespan (in the absence of human impacts) results in relatively stable adult popula-tions (*41*). Animals that are periodic strategists may be dom-inated by relatively few cohorts that survive for years or decades when the stock is unexploited. In an extreme example–with a lifespan of at least 125 years–bigmouth buffalo (*Ictiobus cyprinellus*; Fig. 1I) ranks among the longest-lived

freshwater fishes (*42*). More than 85% of individuals in some bigmouth buffalo stocks were estimated to be at least 80 years old, with river regulation contributing to high recruit-ment variation, yielding about 13 dominant age cohorts be-tween 1894 and 1997. These and many other long-lived freshwater fishes of North America have been considered “rough or trash fish,” with largely unregulated harvest limits and negative societal perceptions (*43*).

The old-animal storage effect of equilibrium strategists (e.g., many birds, mammals, some sharks and bony fishes; Fig. 3) is achieved by a moderate to long lifespan with slow growth and delayed maturation, but generally with a trickle of new recruits joining a stable population dominated by mature individuals (*27*, *32*). Equilibrium strategists tend to dis-play density-dependent survival, growth, and recruitment, with population persistence under conditions of resource limitation, such as within saturated communities *sensu* a *K*-selected strategy (*32*). Equilibrium strategists can be small or large and sedentary or migratory; however, their key attrib-ute is large investment in individual offspring, either in terms of biomass, parental care, or both. In many equilibrium strat-egists, such as humans, nonhuman primates, whales, ele-phants, and pack-hunting carnivores, old individuals are repositories of knowledge (*44*), communicate vital infor-mation to conspecifics, provide enhanced offspring or grand-offspring care (*45*), and regulate culture (*46*) and social struc-tures (*47*) that affect fitness (*48*, *49*). Owing to low intrinsic rates of increase, they are vulnerable to overharvest (*41*) and in some cases even extinction (*50*, *51*) (table S1).

Reproduction and recruitment

One of the most widely studied storage effect mechanisms by which older individuals, both male and female, have been shown to contribute to population viability is via enhanced offspring, grand-offspring, or unrelated juvenile survival (Fig. 2 and table S1). Classic population dynamics and senescence literature generally describes how Fisher’s reproductive value (*52*) is low at birth, peaks near the age at first reproduction, then rapidly declines. Indeed, many species conform to this pattern (*53*–*55*). However, this perspective often fails to cap-ture the important reproductive contributions of older indi-viduals–particularly in moderate- to long-lived taxa with low adult mortality, indeterminate growth or extended reproduc-tive lifespans where reproductive output declines slowly, re-mains the same or increases (*19*, *36*).

Declines in reproductive output at advanced ages ulti-mately occurs in most wild animals, but examples (table S1) where older, often larger individuals make disproportion-ately large contributions to offspring production, quality, and survival have been documented in most vertebrate classes and some invertebrates. Even post-reproductive individuals have been shown to enhance offspring survival in some cases (*51*, *56*, *57*). Older individuals of many species have higher re-productive output and enhanced allocation of nutritional re-sources to support offspring (*19*, *20*, *58*), sometimes with cumulative intergenerational benefits (*58*). In fish and migra-tory birds, older and larger individuals have been shown to breed or migrate at different times, more frequently, or over longer seasons (*13*, *26*, *59*), connect spawning grounds (*60*), and sometimes lead migrations (*61*, *62*)–all of which may af-fect offspring survival and breeding success. Older mothers of wild mammals generally produce fewer offspring with lower survival (*55*), but not all species conform to this classic pattern of reproductive senescence (table S1). Older mam-mals sometimes increase recruitment (survival to maturity) by enhancing grand-parental (*45*, *56*, *63*) or community sup-port of offspring, such as provisioning access to suitable hab-itat, shelter, food or protection from predators. Perhaps the most well-studied species, and arguably most exceptional in terms of parental and grandparental provisioning of vital post-reproductive contributions (*57*), is humans (Fig. 1E). By caring for grandchildren, grandmothers allow daughters to produce more children that survive and reproduce–referred to as the *grandmother hypothesis* (*63*). The grandmother hypothesis applies to some whales (*45*), and it remains an active area of research to understand why selection favors contin-ued life for individuals that can no longer reproduce.

In contrast to declining reproductive output with mater-nal age observed in most mammals, reproductive output and recruitment of birds can increase with age of parents (*55*, *64*), often due to enhanced care, provisioning of resources or allo-parental care. In ectotherms with indeterminate growth, re-productive output can increase to a very advanced age, and in some cases until the oldest age class (*42*). Reproductive output increases with body size and age in many fishes, rep-tiles, amphibians, crustaceans, and mollusks, but less evi-dence is available for recruitment success and offspring quality (table S1). Some ectotherms show hyperallometric scaling of reproductive output (*19*, *20*), whereby larger and older females produce disproportionately more offspring per gram of body mass. Based on life-history strategy (Fig. 3), we hypothesize that periodic strategists may be more likely to have hyperallometric scaling of fecundity, whereas equilib-rium strategists should invest more in individual offspring quality or care. Older, larger or mid-sized female equilibrium strategists have been shown to produce larger offspring (*65*), or higher quality offspring with better individual growth and survival (*66*), but the prevalence (*67*) and importance of this to population dynamics (*68*) and life-history strategies re-quires further research (Box 2). While there is an extensive literature on enhanced reproductive output of big, old fe-males for conservation of bony fish stocks (*19*, *26*, *69*), quan-titative analyses and direct measurements of the impacts of larger females for recruitment success (*70*) in the wild are needed (Box 2) since it has not been studied for most of the >30,000 species of fish or sharks (*65*), and contrasting evi-dence suggests it is not universally important for population replenishment under harvest (*71*–*73*).

In addition to maternal age effects on reproduction, there is a growing body of literature exploring mechanisms of how old males affect reproduction and population dynamics (ta-ble S1). A host of studies continue to attempt to understand the paradox of why females of many taxa choose to mate with older males despite reported costs related to reduced fertility or offspring fitness (*74*, *75*). For example, larger and typically older males have higher paternity success in species ranging from Atlantic cod (*Gadus morhua*) (*76*) to African savannah elephants (table S1). Given that male parental care is more common than female care in bony fishes, developing a better understanding of paternal age impacts on offspring survival seems a fruitful area for future research (Box 2). Despite the heightened fertility and instances of enhanced offspring fit-ness observed in older males of some taxa, a prevailing trend suggests that their predominant contribution lies in assum-ing crucial social roles. Older males frequently engage in leading collective movements (*77*) and regulating social struc-tures (*49*, *78*). These behaviors wield significant influence on decision-making, thereby exerting impacts on group and off-spring survival.

Behavior, knowledge, sociality and culture

The loss of old individuals and their storage effects can alter the structure of societies, modify fitness-related behaviors and result in the loss of knowledge (table S1). For example, human-caused mortality of wolf pack leaders triggers pack instability (*79*), trophy hunting of large carnivores can cause sexually selected infanticide (*80*), and the selective removal of old African savannah elephants (Fig. 1B) reduces matriar-chal knowledge and male leadership (*77*, *81*), disrupting social dynamics, and exacerbating human‑wildlife conflict (*49*). In other species, old or sick animals may be prone to conflict with humans, but this may not be common and contrasts with evidence showing how younger individuals engage in high-risk behavior and human‑wildlife conflict (*82*).

As animals grow old, their behavior changes (*83*, *84*), their life experience and knowledge often increase (*44*, *56*, *61*) and social dynamics shift (*46*, *48*). The pace-of-life hypothesis (*85*, *86*) attempts to predict links among behavior, metabolic rate and life-history but has received inconsistent empirical sup-port, and criticism particularly within species (*87*). One po-tentially flawed assumption of pace-of-life is that it assumes traits are stable over time, and therefore does not predict be-havior to change over the lifespan of an individual. Assuming metabolic rate and behavior are fundamentally linked (*88*), behavior should change predictably with age, ontogenetic stage and vary among species with contrasting metabolic rates and life-histories (*89*) (Box 2). Older age-classes, onto-genetic stages, or long-lived species which coevolved lower age-specific mortality, slower metabolism and growth may be expected to be more cautious, less active, and less aggressive compared to younger, faster-growing age-classes or species with higher rates of natural mortality. Empirical evidence supports how long-lived species may be more likely to evolve social relationships (*47*), and suggests older individuals often modulate aggression (*49*) and stabilize social structures (*44*, *56*, *81*), but other dimensions of sociality, such as network size and time socializing, can decline with age (*48*).

Individuals of all species may not accumulate knowledge with increasing age (e.g., coral), but greater experience, social learning, and better judgement of some animals appear to meet basic definitions of wisdom (*90*) (Box 2). Learning and the transfer of knowledge from one generation or peer to the next, and guidance based on previous experience is required in many species for survival and adaptation to environmental change. Cultural transmission or socially transmitted knowledge includes both environmental and social infor-mation (*46*). Cultural transmission and experiential knowledge are used to locate water during dry periods, find safe shelters, identify valuable associates, and provide access to novel foods during times of scarcity (table S1). For exam-ple, Elder female and post-reproductive killer whales are more likely to lead collective movements of groups through feeding grounds, especially when food is scarce (*56*). Alt-hough *K*-selected (Fig. 3) mammals, such as killer whales, pri-mates and elephants have received significant research attention, older individuals of a range of taxa, including fish, birds, reptiles and other mammals, store knowledge and transmit important information about food, predators, mi-gration, spawning location, and timing (*61*, *62*) (table S1). If social learning and cultural transmission are important for other taxonomic groups, then fisheries and wildlife harvest of an old-age demographic may have additional perverse im-pacts (*91*). Research on knowledge and cultural transmission in wild animal populations including a wider range of verte-brate and invertebrate taxa and impacts of harvest is war-ranted (Box 2).

Social learning and experience provided by Elders may fa-cilitate effective behavioral responses to environmental change. Behavioral adaptation may be critical for long-lived species since they have a slower capacity, from an evolution-ary perspective, to keep up with the speed of global change (*21*, *23*, *38*). Given the rapidity of environmental changes con-fronting many long-lived species, social mechanisms for transferring knowledge between and within generations may enable long-term

survival. However, the more established patterns of behavior (e.g., migration routes, feeding and breeding areas) of older individuals may also limit their abil-ity or willingness to adjust to unprecedented extreme events,
making these individuals vulnerable to climate change. For this reason, understanding behavioral variation in animal populations and the implications of losing old age-structure is crucial for conservation and forecasting the effects of cli-mate change (Box 2).

Ecosystem structure and function

The loss of old individuals not only erodes reproductive and knowledge-related storage effects of these taxa, but owing to their roles in ecosystems (e.g., food webs, nutrient cycling, and ecosystem engineering), the loss of old animals has im-portant consequences for ecosystem structure and function (table S1). Evidence suggests that human hunting (*25*, *92*) and climate change (*93*) contributed to the loss of large animals during the Pleistocene and Holocene. The transition to a non-megafaunal world altered community structures as well as trophic and nutrient dynamics, sometimes resulting in eco-system change. Here we focus on a similar but on-going change to ecosystem structure and function caused by deple-tion of old, often large-bodied, individuals during the Anthro-pocene (*10*, *50*, *94*).

In many aquatic ecosystems, short-lived opportunistic strategists comprise the bulk of primary producer biomass, while higher consumers are often longer-lived periodic or equilibrium life-history strategists (Fig. 4). In undisturbed marine food webs (*39*, *95*, *96*), opportunistic phytoplankton, algae, zooplankton, other invertebrates and small fishes with short generation times and fast population turn-over rates are consumed by longer-lived fishes, sharks and whales. Ow-ing to the slower population turn-over and higher adult sur-vival of large and long-lived consumers (*95*) when compared to their small prey, there exists what we refer to as a “life-history trophic ratchet.” This ratchet can result in the incre-mental accumulation of standing biomass at higher trophic positions composed of long-lived species with slower popula-tion turn-over and low natural mortality in the absence of human impacts. We hypothesize that: 1) the ratchet effect on standing biomass accumulation increases with the longevity of consumers and is greatest in undisturbed ecosystems; and 2) stability provided by long-lived consumers reduces tem-poral variability in community trophic structure (Fig. 4).

The life-history trophic ratchet provides one explanation for top-heavy food webs wherein consumer standing biomass can be equal to or greater than primary producer standing biomass (*96*-*98*). Despite losses of energy with increasing trophic level which leads to decreasing rates of production, a higher standing stock of biomass of animal consumers in comparison to primary producers (Fig. 4) is predicted by the-ory when consumers are much larger and longer-lived than their prey, and when these larger mobile consumers obtain food resources from multiple food webs (*95*, *96*, *99*). Tropical rivers accumulate high standing biomass, not only at the highest trophic positions, but also in lower trophic positions that have many large, long-lived herbivorous, detritivorous and omnivorous fishes (*100*). In contrast to aquatic ecosys-tems, the primary producers of old-growth forests are ex-tremely long-lived, and therefore accumulate carbon and very high standing biomass in old trees (*101*) that are vulnerable to overexploitation. The structure of ‘pristine’ ecosystems is debated and difficult to estimate, but it is clear that abun-dance and biomass accumulation of large, old animals in many ecosystems is greatly diminished in comparison to his-torical conditions (*1*, *3*, *39*, *102*, *103*). Overexploitation of old fish and wildlife can reduce stability and resilience while al-tering food web structure (*13*-*15*, *39*).

Anthropogenic impacts on large animals with a slow pace-of-life (*104*, *105*) can increase the dominance of short-lived, opportunistic life-history strategists and small-bodied con-sumers (Fig. 4) that have higher demographic resilience but high temporal variability (*38*). By contrast, large, long-lived equilibrium and periodic strategists, which tend to be the most valuable fish and wildlife stocks (*18*) that are exploited first, have comparatively low demographic resilience (*38*), but historically high standing biomass and abundance (*3*, *39*, *102*). In food webs affected by over-harvesting or climate change, predator populations often persist, but with fewer old, large individuals and diminished stability and functions within food webs (*4*, *14*, *39*). The loss of the largest, oldest individuals and their trophic roles can result in herbivore or mesopredator release (*106*, *107*) and disrupted ecosystem pro-cesses (*94*). For example, reduced animal size- and age-struc-ture may reduce food web stability (*14*) and affect nutrient cycling (*108*) from local to regional scales (*94*, *109*).

Reductions in the size and biomass of old, typically large, consumers have occurred in many terrestrial, marine, and freshwater ecosystems (table S1). For example, in blue marlin (Fig. 1C) estimates suggest that the probability of catching an old trophy-sized (≥3.5 m) fish has declined by 14 times (*110*). The total biomass of large predatory fish in the open ocean has declined by 36-91% (*103*), the median mass of these ani-mals has diminished substantially since the 1950s (*4*), but the magnitude and extent of these changes appears small relative to the disproportionate loss of old individuals in many ma-rine fisheries (*1*). The depletion of large-bodied and long-lived predators, followed by exploitation of smaller fishes at lower trophic levels, has not occurred in all fisheries or ecosystems, but trophic position and body size declines can be important indicators of altered ecosystem structure and function (*111*-*113*).

The concepts of trophic downgrading (*114*), trophic cas-cades (*115*), fishing down, up and through food webs (*111*, *112*) are based largely on shifts in species composition or aggre-gate consumer biomass. We hypothesize that another poten-tially widespread driver of food web change has been the loss of large, old individuals because: 1) their historical abun-dance and body size in many ecosystems was much greater than it is now (*3*, *4*, *39*, *114*); and 2) larger older individuals may consume different food resources, amounts of food and prey that are often smaller and lower trophic level or occur in different habitats (table S1). Further research understand-ing the potential influence of within species reductions in age and size-structure of consumers on food webs, trophic cas-cades and ecosystem stability, structure and function are warranted (Box 2).

Resistance and resilience to global change

Long-lived species and large old individuals within species have different responses and vulnerabilities to anthropogenic and ecological disturbances (e.g., heat waves, cold spells, fire, floods, disease, hypoxia, food scarcity, altered timing of sea-sonal events) when compared to short-lived species and younger, smaller individuals (table S1). For example, long-lived and large vertebrates are threatened with extinction most often via direct killing by humans (*30*), whereas small-bodied species with limited dispersal tend to have smaller ge-ographic ranges sensitive to habitat loss and modification (*116*, *117*). Nevertheless, habitat loss and related threats, in-cluding climate change, pollution and dam construction, pose serious threats to some long-lived species (*10*, *118*).

Longevity is one of the strongest predictors of population stability in terrestrial and aquatic species (*27*, *35*) because the survival of older individuals of long-lived life-history strate-gists (Fig. 3) buffers their populations from temporal envi-ronmental variability (29). A range of studies on long-lived taxa highlight the importance of storage effects associated with demographic buffering showing how younger age-clas-ses tend to have more variable survival when compared to middle-aged or older age-classes exposed to environmental variation (*21*, *28*, *119*). For this reason, the loss of old age-structure can amplify the destabilizing effects of climate change on animal populations (*119*-*121*). The process of re-moving old age-classes through fishing appears to make pop-ulations more volatile (*15*, *122*, *123*) and less resilient (*13*) as they become increasingly reliant on recruitment from young spawners. Even after accounting for life-history effects, age truncation in exploited fish stocks has been found to increase population variability (*123*). More research is needed to de-velop a holistic understanding of how the loss of older indi-viduals contributes to population volatility. Some evidence suggests that enhanced egg quality or fecundity of larger fe-males may not be particularly important for some popula-tions (*71*), and therefore other mechanisms should also be explored, including altered timing, frequency or location of spawning, age-specific behavioral differences, impaired cul-tural transmission or altered care for offspring. Even in rela-tively short-lived species, such as frogs, where disease can disproportionally affect older ages, the loss of old individuals erodes their ability to withstand interannual recruitment fail-ure and drought (*11*). The heightened sensitivity of age-trun-cated populations to global change may make some species more at risk of extinction (*124*), yet long-lived species also show remarkable life-history plasticity in response to harvest and other anthropogenic pressures (*125*, *126*). How life his-tory strategies and the loss of old individuals, especially from fishing, hunting and climate change, interact to affect popu-lation volatility, resilience, collapse and extinction remain important areas of future research (Box 2).

Long-lived animals have adapted to persist under envi-ronmental conditions of past climates, yet these species have undergone mass extinctions (*127*) and likely are vulnerable to more frequent and severe environmental changes associated with contemporary climate change (table S1). In an analysis of 484 published studies on sea birds and marine mammals (*8*), species with long generation times and narrow thermal niches were most often affected by climate change. Similarly, land mammals with slower life-histories, larger body sizes and an inability to easily access thermal refuges appear vul-nerable to climate change (*9*), and were prone to climate-in-duced extinction in the past (*93*). An analysis of 332 species of marine fish showed how increasing temperature acceler-ates pace-of-life, potentially leading to faster population growth (*128*). Although enhanced productivity in some long-lived ectotherms may be beneficial, critical physiological thresholds of high temperature and low oxygen are being ex-ceeded for many species and causing range shifts, altered phenology, sub-lethal and lethal effects (*129*, *130*). More re-search is needed on age- and body-size-specific physiological and behavioral responses to extreme events (e.g., drought, fire, flood, hypoxia, etc.) and how they affect population dy-namics (Box 2).

Longevity conservation

Humans have caused a decline in old age-classes of wild ani-mal populations whereby many of Earth’s oldest, often larg-est, and most experienced individuals have been eliminated from ecosystems. To ensure the long-term sustainability of populations, ecosystems and ecosystem services, longevity conservation should be included among options for manage-ment of fish and wildlife. In some cases, such as ecotourism, recreational fishing and trophy hunting, the largest and fre-quently oldest individuals are themselves a highly valued commodity.

Recent fisheries models suggest that conservation of old age classes can enhance sustainable production under appro-priate circumstances (*68*, *69*, *119*). The Maximum Sustainable Yield (MSY) paradigm (*131*) has not led to well-managed fish-eries in part because the recruitment of many fish popula-tions fluctuates according to environmental conditions that vary at large spatiotemporal scales (*132*), and this volatility is exacerbated by fishing-induced age truncation (*15*, *122*, *123*). For these reasons, assumptions of density-dependent recruit-ment and the expected surplus production arising from MSY targets (*131*) have been overestimated for many stocks and likely explain why some fisheries collapse. To reduce fisheries volatility and enhance long-term sustainability, fisheries managers must recognize the potential for longevity overfish-ing (*133*) and begin to consider longevity conservation. Given that enhanced reproductive output (*19*) is not the only reason to preserve old age-structure in animal populations, underap-preciated functions related to behavior, knowledge, food web and social interactions of old individuals should be explored in future research (Box 2) and incorporated into fish and wildlife population dynamics models. For example, a recent study (*134*) incorporated social interactions, including bene-fits of old individuals, into population models for African el-ephants and demonstrated how reductions in positive family interactions caused by poaching exacerbated population de-clines.

The ecological importance of old and large individuals is gaining recognition (*17*, *69*, *133*), but despite findings from age- and size-based population models (*134*‐*136*), longevity depletion continues to be an underappreciated issue for nat-ural resource management. A shifting baseline of age-struc-ture for many populations often leads to an erroneous inference that the population is in good condition or recov-ered when abundance, biomass, or range size targets are met–despite depletion of old age classes. Thinning of old age classes based on unrealistic high expectations of compensa-tory responses arising from MSY (*131*) is a common practice for fish and wildlife populations considered to be well-man-aged. Longevity overfishing (*133*) is not yet recognized by any nation or the United Nations Convention on the Law of the Sea as a type of overfishing.

The International Union for the Conservation of Nature (IUCN) Red List does not yet recognize truncated age-struc-ture in criteria for listing threatened species. Longevity con-servation is defined here as the protection of old individuals to maintain or restore the age structure of populations toward baselines and ranges of variability estimated in the ab-sence of human impacts. Age estimation from least-disturbed populations, historical evidence, modeling, expert, local and traditional knowledge, are all useful methods to define base-lines of age structure. Contemporary ecosystems maintained by local communities, including Indigenous Elders often have equal or higher biodiversity than protected areas (*137*), and long-lived animals such as whales, large fish, and carni-vores often hold lore and cultural value. Therefore, longevity conservation may benefit from legal protection of Indigenous cultural values (*138*).

Longevity conservation should prioritize the protection of old individuals from populations of long-lived life-history strategists (Fig. 3), including less well-known forms, such as sponges, corals and animals of deep-sea environments gener-ally (*2*, *22*, *35*), many turtles (*139*), freshwater (*10*, *43*) and ma-rine fishes (*41*), and cold-water sharks (*34*)–all with long lifespans and ecological functions threatened by anthropo-genic pressures. Management and restoration strategies need to focus on within species age and size-based approaches and will require timeframes that extend across years and decades to achieve the overall goal of reducing mortality of old indi-viduals.

Full recovery of age-structure to historical baselines are unlikely to be feasible, or perhaps even desirable for many harvested populations, as well as for species and ecosystems under altered climate conditions. Therefore, alternative man-agement reference points that balance longevity conservation and socio-economic constraints should be considered (*140*). There is vast scope for socio-economic and environmental gains to be made by improved management of old age struc-ture in commercial and recreational fisheries and wildlife harvest (*17*, *41*, *68*, *69*). Conservation and restoration of old age structure can be achieved using proven management strategies. For example, catch-and-release (*141*) and harvest slot limits (*68*, *142*) can be effective in fisheries with high post-release survival. Since it is often not possible to release fish alive from commercial fisheries, time-area closures (*41*), protected areas (*143*, *144*), balanced harvesting (*145*), gear that protects size structure and by-catch reduction devices are management tools that can help to protect old age struc-ture.

In contrast to many commercial fishing methods, the har-vest of large, old animals through hunting and recreational fishing can be individually age- and size-based. Age-based regulations for hunting (*146*, *147*) are being used to manage wildlife (table S1), but evaluation of their effectiveness requires more research (Box 2). Networks of suitably large and connected no-take reserves or time-area closures in terres-trial, marine and freshwater ecosystems (table S1) can be ef-fective tools to protect old age classes. Effective design of protected areas (*143*, *144*, *148*) or time-area management must account for species mobility, future climate change and locations where old individuals are most vulnerable (i.e., feeding and breeding grounds).

Trade-offs and compromises will be necessary to align commercial, recreational, and conservation objectives. Man-agement strategies to protect animal longevity will require means to reduce mortality of old age classes, or even the total banning of harvest for certain long-lived species. Commercial fisheries that supply global food production could see re-duced yields of some species under management strategies that protect longevity, whereas longevity conservation may not be important for sustainable harvest of other species (*71*-*73*). Emerging evidence is beginning to challenge the notion that protecting old animals inevitably results in negative trade-offs in terms of reduced benefits to people. For exam-ple, strategies that protect young and old individuals can out-perform biomass yields from traditional fisheries management for species that have high reproductive hyper-allometry (*19*, *68*, *69*). Continued development of age- and size-based harvest management solutions (*68*), models (*134*, *136*), and indicators (*110*, *135*) for fisheries and wildlife man-agement warrants research attention (Box 2). Old animals play a vital role in the maintenance of biodiversity and eco-system services and therefore longevity conservation requires dedicated policy directives, political motivation and careful management.

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Fig. 1. Examples of species where older individuals have been overexploited or make unique contributions to populations, ecosystems, knowledge or culture. (**A**) Antarctic glass sponge, *Anoxcalyx* (*Scolymastra*) *joubini*; (**B**) African savannah elephant, *Loxodonta africana*; (**C**) blue marlin, *Makaira nigricans*; (**D**) freshwater sawfish, *Pristis pristis*; (**E**) humans, *Homo sapiens*; (**F**) estuarine crocodile, *Crocodylus porosus*; (**G**) palm cockatoo *Probosciger aterrimus*; (**H**) lion, *Panthera leo*; (**I**) bigmouth buffalo, *Ictiobus cyprinellus*. Photos reproduced with permission from: (A) Bill J. Baker; (B) Phyllis Lee; (C) Marvin Bethune and Allen Andrews; (D) Sharks And Rays Australia citizen science contribution; (E) www.pexels.com; (F) Church Missionary Society Australia; (G) Christina Zdenek; (H) Phyllis Lee; (I) Alec Lackmann.

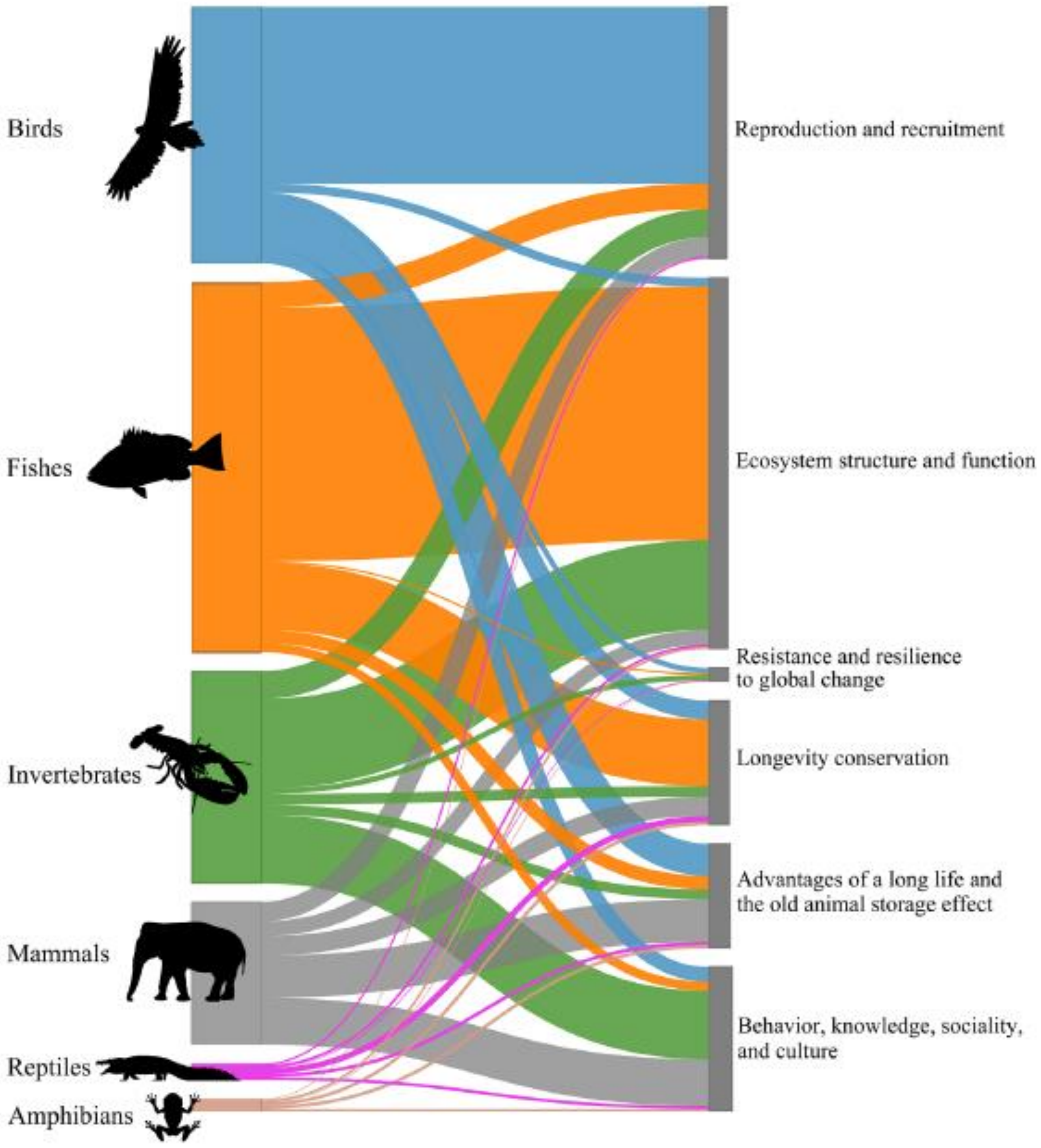

Fig. 2. Most studied topics and taxa related to old-animal ecology and conservation which emerged from text-mining and topic modelling of peer-reviewed papers. Methods used in the topic model analysis are described in the supplementary materials.

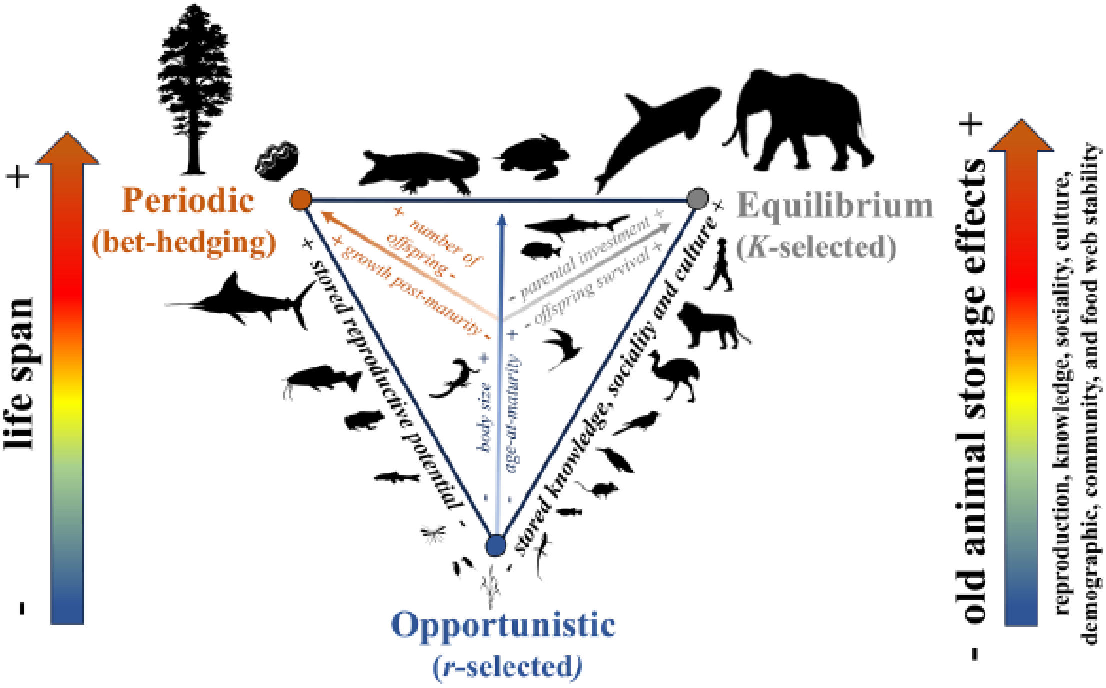

Fig. 3. Scaling of life-history traits and strategies with life span and old animal storage effects. Old individuals of periodic and equilibrium life-history strategists accumulate increasing standing biomass, reproductive potential, knowledge or other fitness-related traits (e.g., increasing body size) over long time periods which can facilitate culture and stabilize social hierarchies, populations and food webs. Opportunistic grasses and periodic old-growth giant sequoia trees (*Sequoiadendron giganteum*) are illustrated for comparison with animal life-histories.

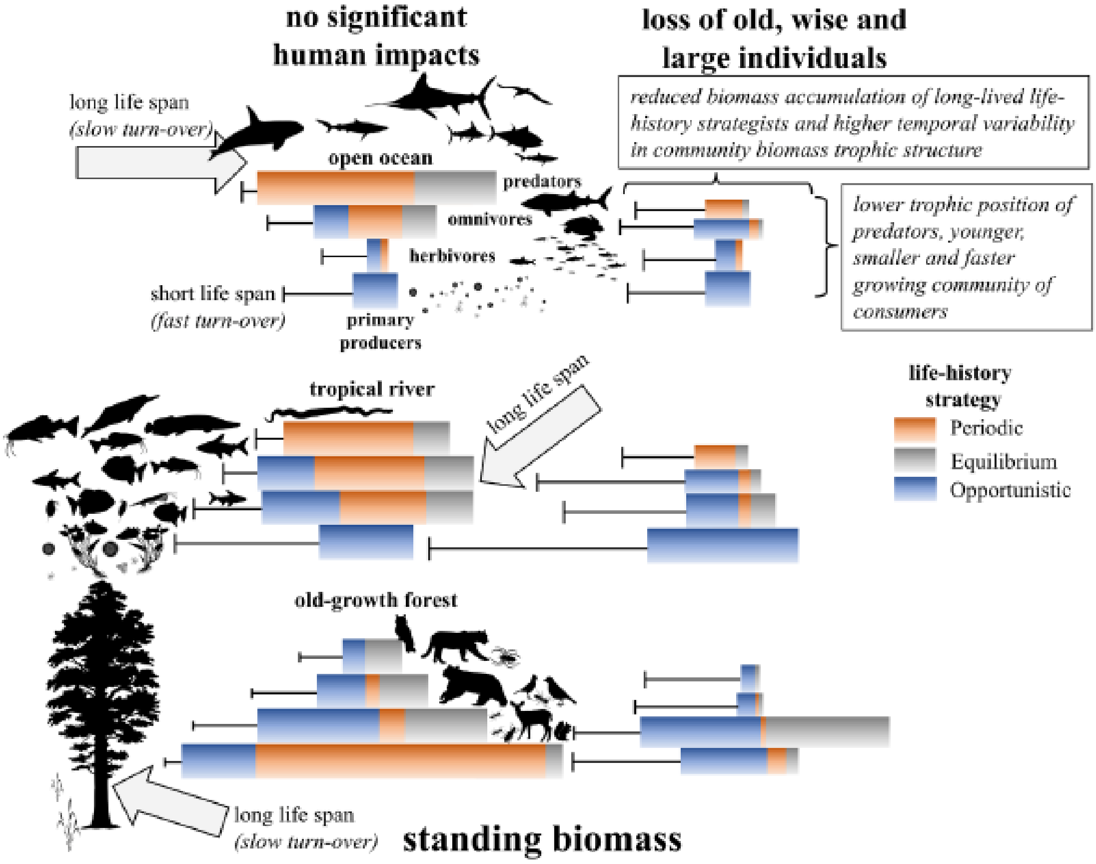

Fig. 4. Generalization of trophic pyramids of standing biomass in open ocean, tropical river and old-growth forest ecosystems. In natural environmental settings, populations accumulate high standing biomass at trophic positions where large, long-lived equilibrium and periodic life-history strategists are positioned. In food webs where old, experienced or large individuals have been over-harvested or reduced because of anthropogenic pressures, community structure and stability are reduced. Error bars represent hypothesized temporal variability in standing biomass.