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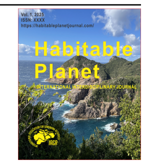

The four stages of the Sixth Mass Extinction

Thomas J. Algeo*[a,b,c,d] and Shucheng Xie[b,e]

[a] *Department of Geosciences, University of Cincinnati, Cincinnati, OH 45221-0013, USA*
[b] *State Key Laboratory of Geomicrobiology and Environmental Changes, China University of Geosciences, Wuhan 430074, China*
[c] *State Key Laboratory of Geological Processes and Mineral Resources, China University of Geosciences, Wuhan 430074, China*
[d] *State Key Laboratory of Oil and Gas Reservoir Geology and Exploitation, Chengdu University of Technology, Chengdu 610059, China*
[e] *Hubei Key Laboratory of Environment and Culture in Yangtze Regions, China University of Geosciences, Wuhan 430074, China*

ABSTRACT

The Earth stands on the brink of another global biocrisis, commonly dubbed the Sixth Mass Extinction (SME). Relative to earlier mass extinctions, it is unique in being a carbon-release event with a bioevolutionary trigger, i.e., the development of technology to an extent that gives humans near-ubiquitous influence over the Earth's climatic, environmental, and biospheric systems. Given that this biocrisis is playing out in real time, it is possible to gain an unparalleled understanding of its evolutionary trajectory and, in particular, the multiple stages through which it is passing. Having started slowly and in a punctuated manner, the pace of the SME has accelerated sharply in the last 100–200 years, and its peak may be no more than a few hundred years away. Although not sharply delineated in time, the four stages of the SME are: Stage 1—hunting and overexploitation (∼50–0.25 ka); Stage 2—habitat loss (∼0.25 ka to present); Stage 3—climate change and alien species invasions (∼0.1 ka to the near-future); and Stage 4—ecosystem collapse (middle future). Each of the first three stages were associated with a technological development that initiated and contributed to coeval biodiversity declines, e.g., advances in early human hunting technology (Stage 1), the spread of agriculture and animal husbandry (Stage 2), and industrialization and combustion of fossil fuels (Stage 3). The fourth stage, ecosystem collapse, is unlikely to require another human developmental trigger—rather, it will come about spontaneously in response to widespread, intense degradation of habitats and biotic communities by human pressures.

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Research Highlights

- The Earth stands on the brink of a major biocrisis termed "The Sixth Mass Extinction"
- It began ca. 50 kyr ago as modern humans spread globally, decimating megafauna
- In recent centuries, extinctions due mainly to habitat loss linked to land use changes
- Today, climate change and invasive species are becoming leading mortality factors
- The final stage of the biocrisis, within a few centuries, will be ecosystem collapse

*Email: Thomas.Algeo@uc.edu (TJA), Xiecug@163.com (SX)

1 Introduction

Most biologists and geoscientists are in agreement that the Earth is on the cusp of a mass extinction. Although popularly known as the 'Sixth Mass Extinction' (SME; e.g., Barnosky et al., 2011; Ceballos et al., 2015) in reference to the well-studied 'Big Five' mass extinctions of the Phanerozoic Eon (Sepkoski, 1996), it has been more formally designated the 'Late Quaternary Mass Extinction' (LQME; Algeo and Shen, 2024). According to the International Union for Conservation of Nature (IUCN), 784 extinctions have been recorded since the year 1500, and ∼44,000 species are "at risk of extinction" (about 25% of the total number of species assessed as of Dec. 2023; cf. Ceballos et al., 2020). Among the most endangered clades are reef-building corals (44%), amphibians (41%), sharks and rays (37%), and conifers (34%). At least as concerning, if not more so, is a general decline in wildlife populations, e.g., a global decline from 1970 to 2020 of 73% among vertebrates generally, with a larger decline in freshwater (85%) than terrestrial (69%) or marine (56%) numbers (World Wildlife Fund Living Planet Index).

Mass extinctions have both ultimate and proximate causes, the former being the trigger that precipitates the biocrisis, and the latter being one or more specific climato-environmental changes that are the immediate cause of biotic mortality (Algeo and Shen, 2024). In the case of the SME, human evolution is undeniably and without question its ultimate cause—other proposed triggers such as climate change and meteorite showers being either minor secondary factors or completely unsubstantiated by existing data (Alroy, 1999). However, the SME is the product not of the evolution of humans *per se* but of human technology, the latter having given modern humans near-ubiquitous influence over the Earth's climatic, environmental, and biospheric systems. Although the SME shares the characteristic of having a bioevolutionary trigger with the Late Ordovician and Late Devonian mass extinctions and of being a carbon-release event with the end-Permian, end-Triassic, and end-Cretaceous mass extinctions, it is a unique biocrisis in Earth history in being the only one that represents a carbon-release event with a bioevolutionary trigger (see classification of Algeo and Shen, 2024).

With regard to proximate causation, many biocrises are associated with multiple concurrent climato-environmental changes, affecting light levels, temperature, ocean-redox conditions, acidity, nutrient availability, and siltation, among others—all of which are generally harmful to marine and terrestrial ecosystems (Algeo and Shen, 2024). In many cases, it is difficult or impossible to tease apart the effects of multiple concurrent changes of this type and determine their relative influences during an extinction event, although statistical analysis of large databases can potentially yield insights (e.g., Epps et al., 2004). In the case of the SME, real-time observation permits an exact evaluation of the climato-environmental effects contributing to the biocrisis, and how these effects are evolving through time. Because of the far higher resolution and relative completeness of information pertaining to the SME, it is possible to identify multiple sequential stages in its overall dénouement, a level of insight that is typically impossible for deep-time extinctions in which data resolution is typically no finer than 10^4–10^5 yr, and in which temporal changes in the pattern of climato-environmental forcings can be distinguished in only a rudimentary manner (e.g., Xie et al., 2005; Dal Corso et al., 2022). In contrast, aspects of the SME that have played out during historical times can be almost exactly dated, and even events in its early stages in prehistory around 50 kyr ago can be constrained to within a few thousand years (e.g., Miller et al., 2005). The high level of temporal resolution for the SME offers unparalleled insight into how this biocrisis has unfolded through time.

The SME is a complex, multistage event that commenced at least 50 thousand years ago (Fig. 1; Algeo and Shen, 2024). The main proximate causes of extinction have changed over this time interval and are likely to continue changing in the near future. In its initial stage (Stage 1, ∼50–0.25), faunal extinction was due primarily to overexploitation of prey species, or to loss of top predators that were in competition with human hunters. In its present stage (Stage 2, 0.25–0 ka), faunal extinction is due primarily to habitat loss, as humanity has transformed broad swathes of land surfaces to its own purposes, creating artificial ecosystems that are capable of sustaining only a fraction of the biodiversity of natural ecosystems. The first extinctions due to the direct effects of climate change have begun (Stage 3), and in the near future (i.e., over the next century or two), such changes are likely to cull many species as they become increasingly maladapted to rapidly shifting climatic zones, with a massive influx of alien invasive species playing an important secondary role. In the final stage of the SME (Stage 4; speculatively, ca. 100–500 yr in the future), other causes will be overtaken by wholesale ecosystem collapse, as is thought to have occurred during the largest biocrises of the past (e.g., Dal Corso et al., 2022).

The intensity of faunal extinction will almost certainly vary through these stages—while Stage 1 eliminated a significant fraction of large mammals in some regions, total biodiversity loss (as measured in species) was quite small at a global scale—only a fraction of 1% (Fig. 1). Moreover, extinctions during Stage 1 occurred only sporadically through time, as humans first appeared in previously unpopulated regions. The present stage of the SME (Stage 2) has also driven a relatively small percentage of extant species to extinction, representing perhaps 1–2% of total biodiversity (itself an uncertain quantity; Mora et al., 2011),

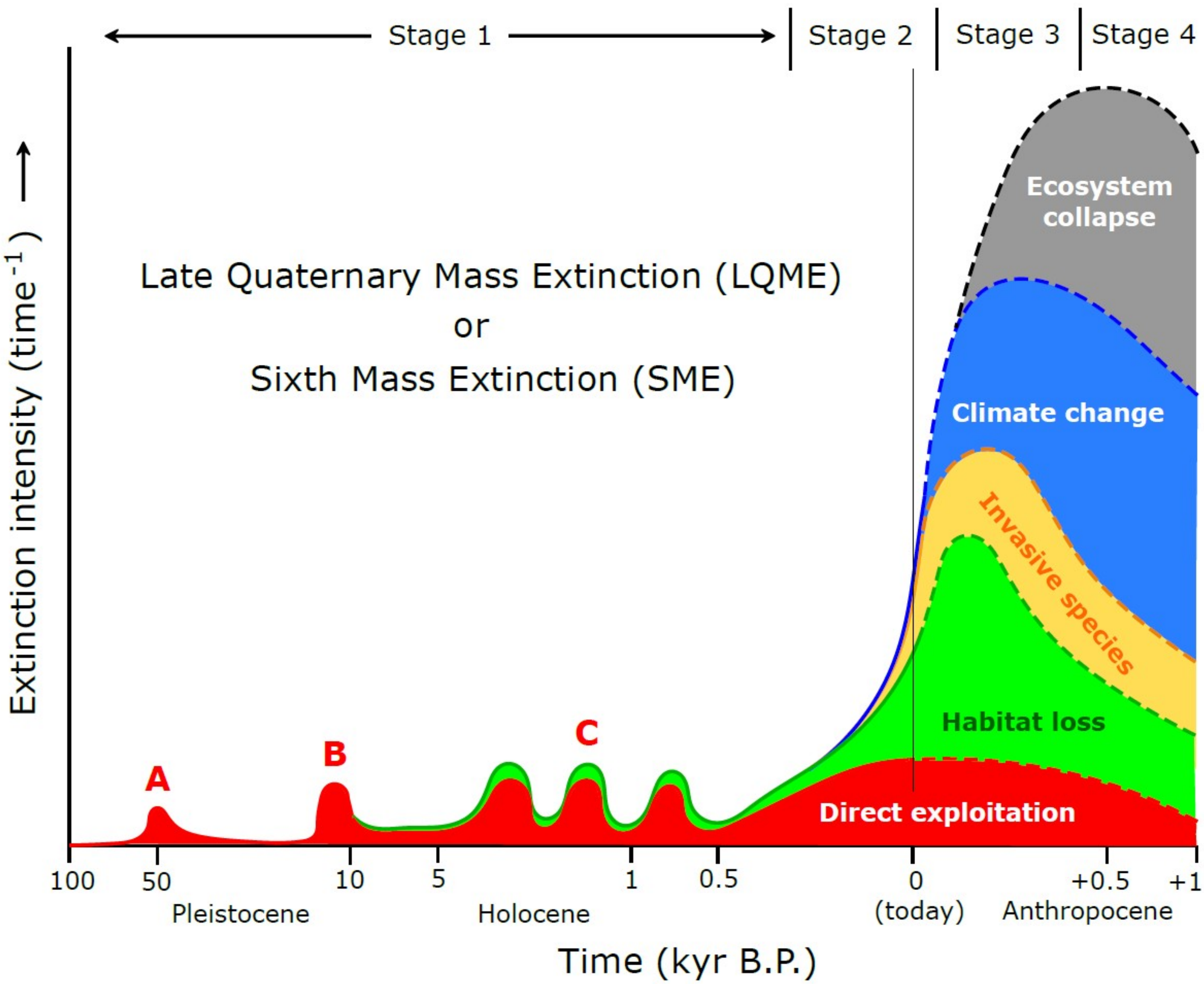

Fig. 1. Four stages of the Late Quaternary Mass Extinction (a.k.a. Sixth Mass Extinction). A, B, and C represent megafaunal extinctions in Australia, the Americas, and the Indo-Pacific region, respectively. Note that both axes have log scales, and that the y-scale is unquantified and relative. From Algeo and Shen (2024).

although with considerable variation among biotic clades, and with substantial uncertainty about the actual extent of the losses. These relatively modest biodiversity losses are belied by the pace of extinction, however, which is far above the natural background level (probably by a factor of 1000× or more; Ceballos et al., 2015; De Vos et al., 2015), representing a rate at which a large fraction of the total number of species on Earth is likely to be lost over the course of the next few centuries (Urban, 2015). Furthermore, the most worrisome aspect of the present stage is that all ecosystems (marine, freshwater, and terrestrial) are being seriously degraded, with large declines in population numbers and range contractions of many species (e.g., Living Planet Index; `https://ourworldindata.org/grapher/global-living-planet-index`), a pattern that presages much higher extinction rates in the not-too-distant future (Dirzo et al., 2014). The final stage of the SME—ecosystem collapse—will almost certainly be the grimmest reaper of all, with the potential to rapidly wipe out a large share—possibly the majority—of total global biodiversity (MacDougall et al., 2013; Bergstrom et al., 2021).

2 Stage 1: Hunting and overexploitation

The impact of humans on Earth's biodiversity may extend back to the dawn of the *Homo* lineage at ~2.8 Ma.

Early humans are thought to have increased the proportion of animal protein in their diet, bringing them into competition with carnivores, possibly contributing to the extinction of sabertooth cats and long-legged hyenas such as *Chasmaporthetes* at ∼2.0–1.5 Ma (Brantingham, 1998; Werdelin and Lewis, 2013). Large herbivore diversity also declined, e.g., the 12 species of elephants and their relatives present in Africa, Europe, Asia, and the Americas during the early Pleistocene were reduced to two by the late Pleistocene (Surovell et al., 2005; Todd, 2006). However, the impact of hunting by early humans was limited to macrofauna, the total number of species impacted was limited, and the role of other factors such as climate change cannot be excluded.

Unambiguous effects of megafaunal exploitation emerged as modern humans (*Homo sapiens*) moved out of Africa into new regions (Hoffecker, 2017), initiating Stage 1 of the SME (Fig. 2A). Animal populations that had not coevolved with humans (as in sub-Saharan Africa) were unprepared to deal with hunters employing advanced strategies and technology, and many species were driven rapidly to extinction, probably within a few thousand years or less following first contact—an idea known as the “Pleistocene overkill hypothesis” (Martin, 1989). Human invasion of Australasia at ∼50 ka was quickly followed by extinction of the Australian Megafauna, including large species of marsupial carnivores, kangaroos, and emus, with both overhunting and fire-transformed landscapes held responsible (Miller et al., 2005) (Fig. 2B). Human invasion of the Americas at ∼15–13 ka led to extinction of dozens of mostly large terrestrial animals before ∼10 ka (Gill et al., 2009; Broughton and Weitzel, 2018) (Fig. 2C) [note: hypotheses invoking bolide impacts or other non-anthropogenic mechanisms for the North American extinctions are based on a misreading of extant evidence and poor reasoning; see Alroy, 1999]. This pattern of human invasion followed by rapid extinction of mostly larger animals impacted many island ecosystems as well: Madagascar at ∼2 ka (Crowley, 2010), New Zealand at ∼0.8 ka (Allentoft et al., 2014), and various Indo-Pacific islands over the past few millennia (Duncan et al., 2013; Spatz et al., 2017) (Fig. 2D). It should be noted that, particularly on islands, the impact of humans was generally amplified or overshadowed by the effects of introduced species such as dogs, cats and rats (Shiels et al., 2014) [see Alien Species Invasions below]. In areas with less well-defined human arrival times, e.g., central and northern Eurasia, megafaunal extinctions occurred sporadically, reflecting an episodicity of first contact with modern human hunters (Stuart, 1999; Stuart and Lister, 2012).

Hunting and overexploitation have continued to drive animal species to extinction or the brink of extinction repeatedly in historical times. The dodo, which lived on Mauritius and a few neighboring islands in the Indian Ocean, succumbed to the pressures of the sailors’ cookpot and the vulnerability of ground nests to rat attacks ca. 1660 A.D., i.e., within about sixty years of first contact (Roberts and Solow, 2003). Rhinos have experienced local extinctions in Southeast and East Asia (Brook et al., 2014) and are presently threatened in their remaining habitats in East Africa and Java (Moodley et al., 2017). In some instances, the carnage has been mostly inadvertent, as in the case of the West Indian manatee, which is slowly succumbing to the effects of pollution in coastal waterways combined with accidental collisions with motorized boats (Runge et al., 2017). Large freshwater animals such as the Yangtze dolphin (Turvey, 2009) have fared particularly poorly owing to a combination of limited habitat range, small population numbers, and the extent of transformation and pollution of their native habitats in continental and coastal water bodies. Such pressures are linked to both expansion of the global human population (which rose ca. 4-fold during the 20^{th} century) and the increasing sophistication of technology available to humans.

3 Stage 2: Habitat loss

Although pressures linked to hunting and overexploitation of species have not abated in recent times, other factors have become more important drivers of the SME. In Stage 2 of the SME (∼0.25–0 ka; Fig. 1), faunal extinction is due primarily to habitat loss, an ongoing process as humanity has transformed broad swaths of land surfaces for its own purposes, creating artificial ecosystems that are capable of sustaining only a fraction of the biodiversity of the previous natural ecosystems (Calizza et al., 2017) (Fig. 3A). The precise starting time for Stage 2 is difficult to pinpoint. Humans are thought to have played a role in habitat changes since their appearance in many areas, e.g., the elimination of large terrestrial herbivores by paleohunters is considered to have fundamentally altered some Pleistocene landscapes (Johnson, 2009). Land-use changes related to conversion of natural landscapes into agricultural and pastural land commenced by ∼10 ka, at the onset of the Agricultural Revolution, yet the initial changes occurred slowly and in limited regions. It is only in the last few hundred years that the pace of land-use change has accelerated sharply (Beyer and Manica, 2020; Fig. 3B), ultimately driven by a rapid rise in the global human population. It is probably only during this recent few-hundred-year interval of accelerated land-use change that impacts have registered as major declines in endemic biotas.

Habitat fragmentation typically accompanies habitat loss. As large areas of pristine habitat become parceled up, biodiversity declines due to habitat degradation, habitat isolation, reduced size and resiliency of local populations, changes in species interactions, and increased exogenous threats, among other factors (Fischer and Lindenmayer, 2007). Extinction cascades are common in land-

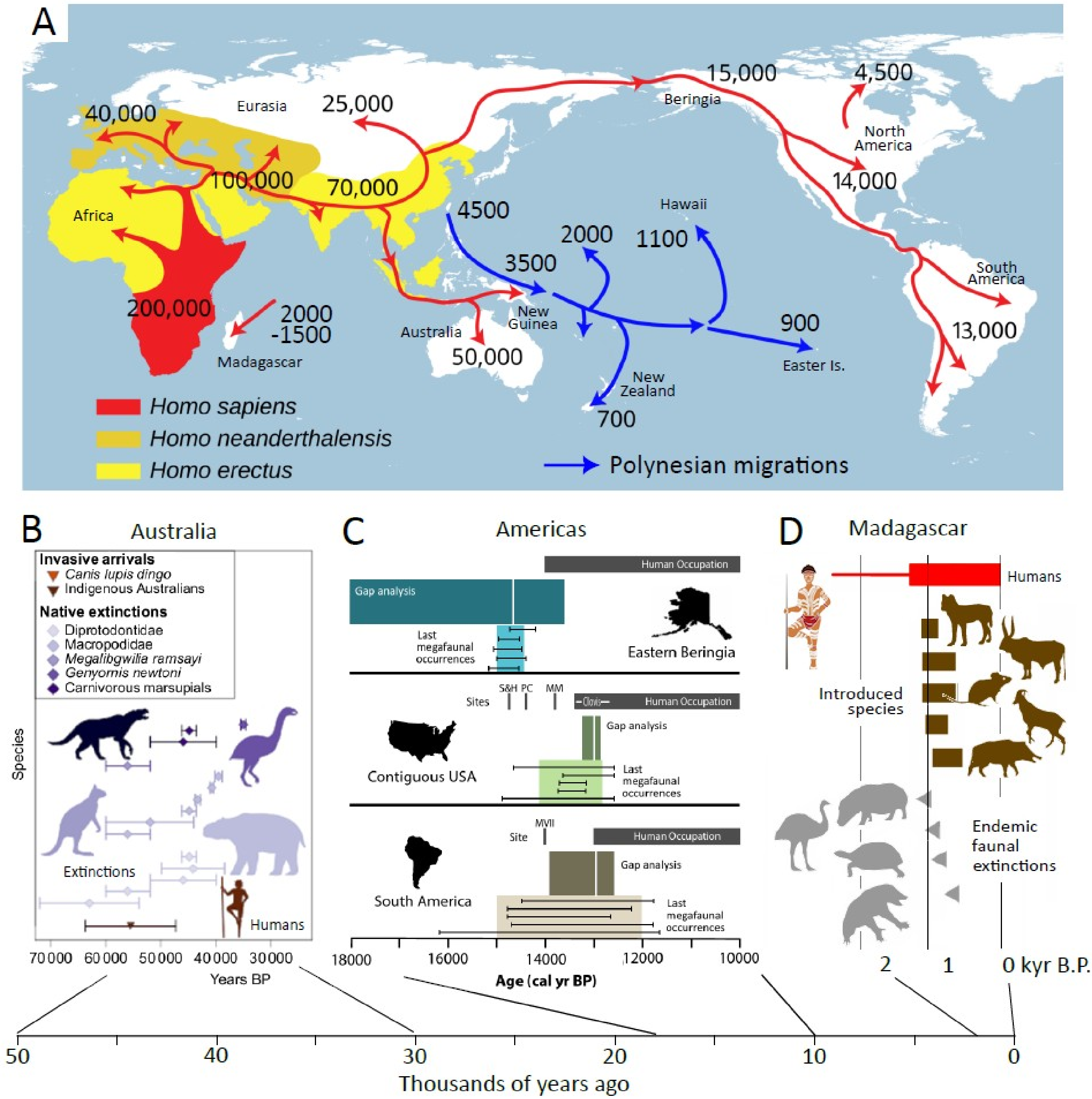

Fig. 2. Timeline of faunal extinctions linked to human migration into previously uninhabited regions (Stage 1 of SME). (A) Global human migrations (all numbers represent years B.P.). Map adapted from Wikipedia pages on "Early human migrations" and "Polynesians". (B–D) Temporal relationships of faunal extinction to human migration in Australia (Gaschk and Clemente, 2022), the Americas (Surovell et al., 2016), and Madagascar (Antonelli et al., 2022).

scapes with low vegetation cover, low landscape connectivity, degraded native vegetation and intensive land use in modified areas, especially if keystone species or entire functional groups of species are lost. This pattern has been

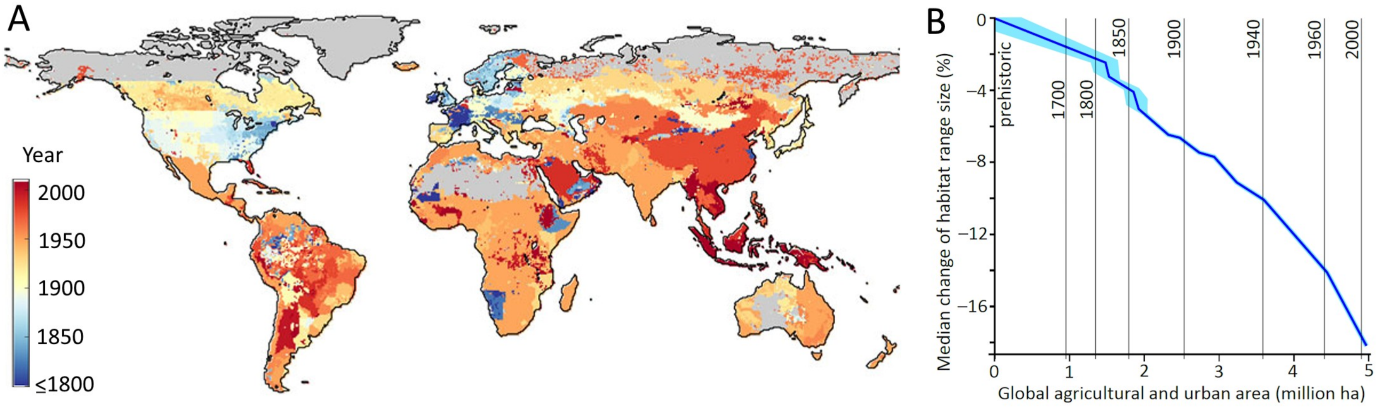

Fig. 3. Habitat loss and reduced species ranges (Stage 2 of SME). (A) Global map showing time of peak conversion of natural habitat to agricultural or urban land (to 2010). (B) Across-species median range loss against cumulative global agricultural and urban area (ages at top correspond to scale of panel A). Note the acceleration of land conversion as well as habitat and range losses toward the present. From Beyer and Manica (2020).

observed in various regions globally, including the Amazon rainforest (Laurance et al., 2018), Borneo (Ocampo-Peñuela et al., 2020), New Guinea (Broekman et al., 2024), and the island of Hispaniola (Hedges et al., 2018). Biodiversity hotspots are especially vulnerable to the effects of habitat fragmentation—among the 25 hotspots surveyed by Brooks et al. (2002), none has more than 33% intact cover compared to a century ago, and the average loss of habitat area exceeds 85%. This is a factor in 50–67% of all threatened plants and 57% of all threatened terrestrial vertebrates being hotspot endemics. Moreover, with global warming [see Climate Change below], fire is becoming an increasingly important agent in habitat loss, e.g., in North America (Driscoll et al., 2021), the Amazon (Feng et al., 2021), and elsewhere.

4 Stage 3: Climate change and alien species invasions

The world is likely on the cusp of large-scale extinctions due to climate change. To date, climate change has mainly caused local extinctions, i.e., loss of local populations of a given taxon leading to range contraction but not complete extinction. However, the first extinctions due to direct effects of climate change are thought to have begun, e.g., the disappearance of the Bramble Cay melomys due to the effects of sea-level rise on its island habitat (Woinarski et al., 2015). In the near future (i.e., over the next century or two; Fig. 1), climate change is likely to cull many species as they become increasingly maladapted to rapidly shifting climatic zones (Thomas et al., 2004; Cahill et al., 2013; Lawlor et al., 2024), representing Stage 3 of the SME. Climate change is likely to interact with other anthropogenic impacts, such as overexploitation and habitat loss, to intensify the biotic impacts on both local and global scales (Jetz et al., 2007; Hof et al., 2011).

The biotic impacts of climate change are multifarious. Global warming is causing isotherms to migrate toward both poles at a rate of $\sim$27.5 km per decade (Burrows et al., 2011), in response to which both terrestrial and marine species are shifting toward higher latitudes (Parmesan and Yohe, 2003; Deutsch et al., 2008; Pauchard et al., 2016; Lawlor et al., 2024; Fig. 4A). For terrestrial species, such shifts have negative impacts including increased metabolic energy demands, decreased activity time, and heat-avoidance behavior (Kearney et al., 2009), changing neonatal gender ratios (among some reptiles) (Mitchell and Janzen, 2010), disconnections from host and pollinator species (Memmott et al., 2007; Schweiger et al., 2012), and enhanced activity of pathogens and competitors (Tylianakis et al., 2008; Bonelli et al., 2011). Warming can result in mistimed photoperiod cues among plants in temperate and polar regions (Bradshaw and Holzapfel, 2010), and seasonal shifts can also affect biorhythms among animal species (Visser et al., 1998). Competing environmental stresses can lead to habitat shifts counter to what might be expected from temperature change alone, e.g., downslope movement by plants to track a moisture regime despite the resulting adverse temperature effects (McLaughlin et al., 2002; Crimmins et al., 2011; Fig. 4B). In aquatic settings, increased water temperatures lead to increased metabolic demand for oxygen (Pörtner and Knust, 2007) while simultaneously reducing the dissolved oxygen content of water (Breitburg et al., 2018), as well as to reduced embryo viability, pathogen spread, changes in upwelling intensity (for seabirds feeding on fish), and bleaching and symbiont loss among corals (Cahill et al., 2013). Although climate change is commonly viewed from the

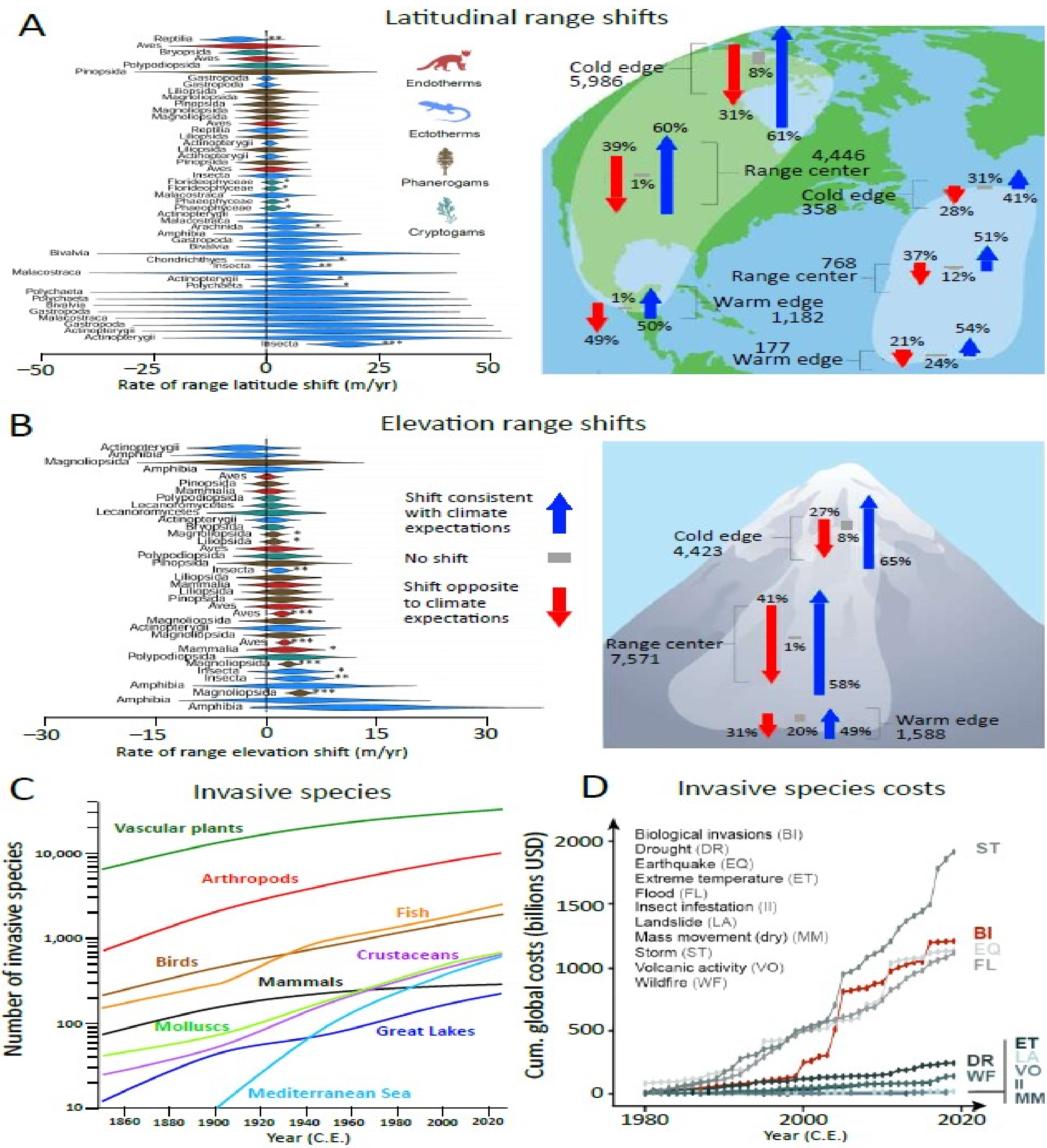

Fig. 4. Climate effects and invasive species (Stage 3 of SME). Climate-driven shifts in (A) range latitude and (B) range elevation of various biotic clades (spindle diagrams from Lenoir et al., 2020; map and cartoon from (Lawlor et al., 2024)). (C) Numbers of invasive species by taxonomic clade (compiled from Seebens et al., 2021), with additional data for the Great Lakes (from Ricciardi, 2001) and the Mediterranean Sea (invasions via the Suez Canal starting in 1869; from Boudouresque, 1999). The near-linear distributions on a log scale mean that invasive species numbers are rising nearly exponentially, mimicking the pattern of global temperature increase since the year 1800. (D) Global costs of invasive species (= BI, shown in red) (Turbelin et al., 2023).

perspective of temperature or rainfall, other environmental factors including windiness/storminess, sea-level rise, salinization of coastal water bodies, and upwelling intensity and nutrient levels in aquatic systems are also important.

Environmental changes commonly lead to an unleashing of pathogens (Harvell et al., 2002; Walika et al., 2023). For example, global warming has been linked to the spread of the chytrid fungus *Batrachochytrium dendrobatidis*, which has decimated amphibian populations globally (Pounds et al., 2006; Kilpatrick et al., 2010; Hof et al., 2011), the disease pasteurellosis among bovids (Ytrehus et al., 2008), and various plant pathogens (Raza and Bebber, 2022). Human agroindustrial processes have probably contributed to the spread of other pathogens such as avian influenza, which is currently decimating poultry farms in the U.S. (Blagodatski et al., 2021). Numerous neopathogens have affected human populations in recent years, including those that cause West Nile fever, severe acute respiratory syndrome (SARS), avian influenza, and monkeypox (Smith et al., 2014). The potential contribution of pathogenic outbreaks to near-future extinctions is difficult to evaluate because, unlike paleoenvironmental changes, ancient disease vectors generally leave few traces. Substantial evidence exists of proliferations of microbial life in the immediate aftermath of earlier mass extinctions (Xie et al., 2005; Luo et al., 2024), but there are inherent challenges to studying paleopathogens in deep-time systems (Xie et al., 2023).

Although direct environmental effects (e.g., rising temperature, decreasing rainfall) are often cited as key stressors in single-taxon studies, ecosystem-scale analyses suggest that the main driver of mortality is changing species interactions, often resulting in decreased food availability (Harley, 2011; Cahill et al., 2013). Reasons for decreased food availability include elimination of a prey species for carnivores (Durance and Ormerod, 2010), loss of vegetation species for herbivores (Epps et al., 2004), loss of a host species for parasites, loss of pollinators for flowering plants (Memmott et al., 2007), and enhanced competition at any trophic level (Wethey, 2002). In the 18th century, human hunting of sea otters led to a population explosion of sea urchins, which in turn largely eliminated the kelp that was central to the diet of Steller's sea cow (*Hydrodamalis gigas*), being a major factor in extinction of that species (Blackburn et al., 2019; Roopnarine et al., 2022). Another example of anthropogenic disturbance of natural ecosystem equilibria is overharvesting of the predators (both vertebrate and invertebrate) on the Crown-of-Thorns Starfish, contributing to massive outbreaks that have devastated parts of the Great Barrier Reef (Cowan et al., 2017). The potential extinction of keystone species, i.e., taxa that play a critical role in maintaining ecosystem structure, affect many other organisms, and have a disproportionately large effect on their natural environment, is of particular concern (Jordán, 2009). Changes in species interactions and loss of keystone species will be a harbinger of general ecosystem collapse [see Ecosystem Collapse below].

A major contributory factor to Stage 3 extinctions is likely to be alien species invasions (Valéry et al., 2008; Fig. 4C). Although the role of invasive species is nominally distinct from that of climate change, in practice, bioinvasions are driven by the same factor as climate change: utilization of fossil fuels, which has greatly accelerated bioinvasions (both intentional and inadvertent) as people and goods are transported globally. The numbers of introduced species have risen dramatically since the mid-19th century, a product of increased movements of people and goods globally (Jeschke and Strayer, 2005) (although some species invasions are 'natural' in the sense of not requiring a human agent; Valéry et al., 2008). The problem is substantial: ~50% of introduced species become established, and ~50% of those that become established succeed in spreading (Jeschke and Strayer, 2005), although success rates are higher for some species such as the American Gray Squirrel (70–80%) (Mazzamuto et al., 2021).

The vectors of alien species invasions are varied (Blackburn et al., 2019). First, many such species arrived as stowaways, mostly in ship-borne or airborne cargo. The brown tree snake (*Boiga irregularis*) has caused the local extinction of more than half of Guam's native bird and lizard species, two of Guam's three native bat species, and several global extinctions (Rodda and Savidge, 2007). The black rat (*Rattus rattus*), which has directly contributed to the extinction of hundreds of species of birds, mammals, reptiles, invertebrates, and plants, especially on islands (Shiels et al., 2014). In North American freshwater and marine habitats, invasive fish species number in the hundreds (Rhyne et al., 2012; Fig. 4C). Second, some invasions are the product of intentional introductions gone wrong, e.g., the rosy wolfsnail (*Euglandina rosea*) was widely introduced across the South Pacific as a biocontrol agent of the giant African land snail (*Achatina fulica*) but has instead preyed on other endemic snails, and it is now thought to have been directly responsible for the extinction of at least 134 snail species (Gerlach et al., 2021). The Kudzu vine, endemic to Japan, was intentionally planted widely in the U.S.A. during the Dust Bowl era (ca. 1930–1945) to control soil erosion but became a major problem owing to its rapid growth and smothering of other plants (Forseth and Innis, 2004). Third, the exotic pet trade is a major factor in the spread of invasive vertebrate species (Lockwood et al., 2019), accounting for ~85% of 140 invasive species of reptiles and amphibians in Florida (Krysko et al., 2011) and ~70% of invasive mammal species in Brazil over the past 30 years (Rosa et al., 2017).

Invasive species can significantly alter ecosystem processes and functions (Vilà et al., 2011; Bellard et al., 2021). A successful invasion invariably changes species interactions and energy flows within the affected region. Invasive species negatively affect native species through competitive exclusion, niche displacement, predation, parasitism, disease, hybridization, and introgression, among other processes (Jeschke and Strayer, 2005; Mazzamuto et al., 2021). For example, the American gray squirrel, known for its adaptability and aggressiveness, rapidly displaced native red squirrels in the British Isles through competitive exclusion (Bertolino, 2008). The frequency with which invasive species play a role in the threatened status of endemic species is uncertain, with estimates ranging up to ~50% (Dueñas et al., 2018).

Many invasive species are highly destructive and costly to control (Turbelin et al., 2023; Fig. 4D), e.g., the fire ant (Ascunce et al., 2011), zebra mussel (Miehls et al., 2009), Asian carp (Phelps et al., 2017), and Asian hornet (*Vespa velutina*; Pedersen et al., 2025), among others. The Asian hornet, which arrived in France in a cargo shipment about 20 years ago and has since spread across much of Europe, is an opportunistic carnivore, consuming hundreds of different insect taxa, including many pollinators, among them some such as the bumblebee that are critical for pollination of commercial crops. Invasive plants also pose substantial risks to commercial crops (Driscoll et al., 2014). Eradication of invasive species is possible, but most successful instances have been on small islands rather than larger islands or continents, although small populations have been eradicated on continents, as for Pallas's Squirrel in Belgium (Adriaens et al., 2015). To put the issue of invasive species into perspective, it might be well to remember that modern *Homo sapiens*, originating from NE Africa, was an invasive species that spread through Europe and Asia, displacing Neanderthals and Denisovans, before establishing itself in regions that were previously free of humans such as the Americas and most oceanic islands.

5 Stage 4: Ecosystem collapse

In its final stage (Stage 4), the SME is likely to be characterized by wholesale ecosystem collapse (MacDougall et al., 2013; Bergstrom et al., 2021; Fig. 1), as has occurred during the largest biocrises of the past (e.g., Dal Corso et al., 2022). Ecosystem collapse is "a change from a baseline state beyond the point where an ecosystem has lost key defining features and functions, and is characterized by declining spatial extent, increased environmental degradation, decreases in, or loss of, key species, disruption of biotic processes, and ultimately loss of ecosystem services and functions" (Bergstrom et al., 2021). Although ecosystems have a degree of autostabilization that provides resiliency, perturbations that are large or rapid enough to cross a critical threshold (i.e., an 'ecological tipping point') will cause ecosystem collapse (Canadell and Jackson, 2021; Fig. 5A). This process is generally irreversible and leads to the appearance of a new ecosystem, one that may retain some characteristics of the previous ecosystem yet will have greatly altered structure and function, often in a diminished form (Keith et al., 2013). Whereas Stages 1 to 3 of the SME were each triggered by a specific development among humans (i.e., hunting technology and migration for Stage 1, the Agricultural Revolution for Stage 2, and the Industrial Revolution for Stage 3), the process of ecosystem collapse during Stage 4 will not require such a specific trigger. Rather, the cumulative stresses associated with the earlier stages of the SME will come about spontaneously in response to widespread, intense degradation of habitats and biotic communities by human pressures.

Local ecosystem collapse is already widespread and includes well-known examples such as the demise of the Newfoundland cod industry due to overfishing (Hutchings and Myers, 1994), the Aral Sea biome through desiccation (Micklin, 2007; Fig. 5A), and continental-shelf sea-ice hunting platforms used by Arctic polar bears (Laidre et al., 2018). Across Australia, the Great Barrier Reef and 18 other regional ecosystems are in partial states of collapse due to a combination of global climate change and human impacts (Bergstrom et al., 2021). Ecosystem collapse in a few regions may lead to increased productivity, e.g., collapse of Arctic sea ice has the potential to enhance a phytoplankton-supported food chain (Vincent and Mueller, 2020), but most collapses lead to losses of diversity and productivity (Hooper et al., 2012). Terrestrial ecosystems typically underwent steep declines in complexity (averaging ~50%) through loss of food web links after the arrival and expansion of human populations (Fricke et al., 2022).

Given that human and natural ecosystems are reciprocally linked, ecosystem collapse will affect human societies by altering flows of ecosystem benefits to people (Newton et al., 2024). For example, the arrival of modern humans in Neolithic Europe and SW Asia is thought to have led to transient population peaks resulting from overtaxing natural ecosystems, whose collapse then led to sharp reductions in human population numbers (Downey et al., 2016). The end result was a partial ecosystem collapse linked to forest clearance and introduction of non-native plant and animal species (Newton et al., 2024). This phenomenon is well documented for Easter Island, where Polynesians arrived ca. 1100 A.D., experienced a population boom within a few hundred years, and subsequently deforested the island, severely disrupting terrestrial ecosystems and limiting access to marine resources (e.g., due to lack of wood for canoe/ship building), which is thought to have caused a 90–95% fall in population numbers in the few hundred years before Europeans arrived (Diamond, 2011; Fig. 5B).

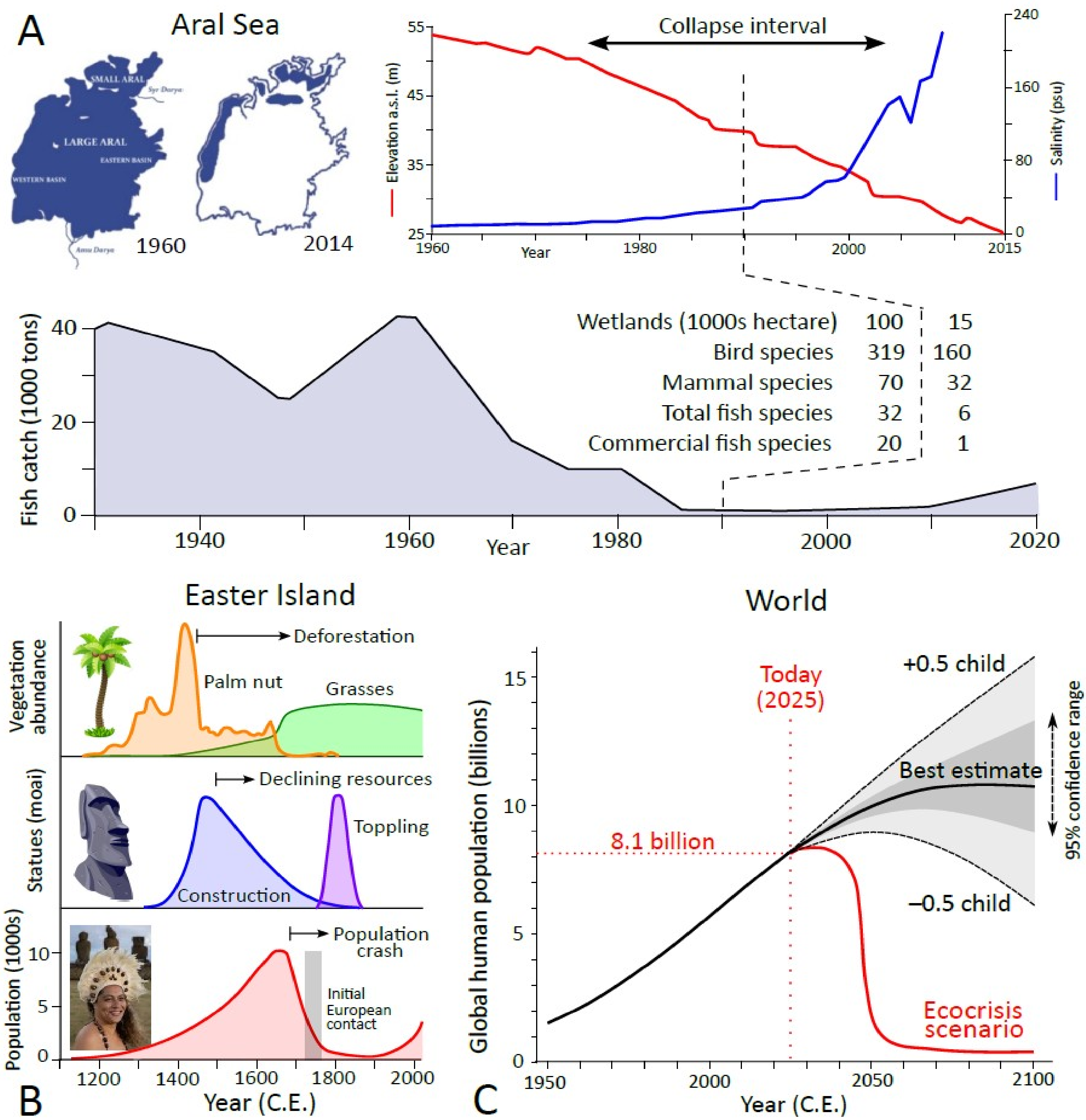

Fig. 5. Examples of local ecosystem collapse: (A) Aral Sea (sources: Micklin, 2007; Micklin and Aladin, 2008; Ermakhanov et al., 2012; Aladin et al., 2019), and (B) Easter Island (sources: Mieth and Bork, 2005; Lipo and Hunt, 2006; Diamond, 2011; Stevenson et al., 2015; DiNapoli et al., 2020; O'Leary, 2021). Pre-contact population numbers are uncertain, with the maximum variously estimated at 10 to 30 thousand. (C) Projected global human population trends to 2100, including best estimate with 95% confidence range, and a broader range representing a global increase/decrease in fertility of 0.5 child per woman (source: U.N., 2022). The "ecocrisis scenario" envisions a population crash driven by the catastrophic effects of global warming, reduction of food supplies, global warfare, and destruction of infrastructure and communication on which global civilization depends (cf. Lennon, 2022); it is purely speculative but consistent with a worst-case outcome of present ecological trends leading to Stage 4 of the SME.

We must take care that anthropologically driven biological and ecological impoverishment of Earth does not lead to a similar fate for the human race as a whole (Fig. 5C).

6 Conclusions

The present-day biocrisis, commonly known as the Sixth Mass Extinction (SME), is a protracted event comprised of several stages. The primary biospheric stresses were hunting and overexploitation during Stage 1 (∼50–0.25 ka), shifting to habitat loss during Stage 2 (∼0.25 ka to present). Stage 3, which has just begun, is characterized by biodiversity losses to climate change and alien species invasions, and Stage 4, which lies ahead of us, will be marked by widespread ecosystem collapse. The ultimate cause of the SME is the development of technology to an extent that gives humans near-ubiquitous influence over the Earth's climatic, environmental, and biospheric systems. Stage 1 was triggered by advances in early human hunting technology, Stage 2 by the spread of agriculture and animal husbandry, and Stage 3 by industrialization and combustion of fossil fuels. The fourth stage, ecosystem collapse, is unlikely to require another human developmental trigger—rather, it will come about spontaneously in response to widespread, intense degradation of habitats and biotic communities under human pressure.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Credit Author statement

Thomas Algeo: Conceptualization; Investigation; Visualization; Writing—original draft.

Shucheng Xie: Funding acquisition; Writing—review & editing.

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