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Review

Turtles and Tortoises Are in Trouble

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Turtles and tortoises (chelonians) have been integral components of global ecosystems for about 220 million years and have played important roles in human culture for at least 400,000 years. The chelonian shell is a remarkable evolutionary adaptation, facilitating success in terrestrial, freshwater and marine ecosystems. Today, more than half of the 360 living species and 482 total taxa (species and subspecies combined) are threatened with extinction. This places chelonians among the groups with the highest extinction risk of any sizeable vertebrate group. Turtle populations are declining rapidly due to habitat loss, consumption by humans for food and traditional medicines and collection for the international pet trade. Many taxa could become extinct in this century. Here, we examine survival threats to turtles and tortoises and discuss the interventions that will be needed to prevent widespread extinction in this group in coming decades.

Introduction

Turtles and tortoises are among the most remarkable organisms on Earth. The chelonian shell is a 220-million-year-old adaptation that predates the origins of mammals and birds [1,2] and has contributed to the success of turtles and tortoises in terrestrial, freshwater and marine ecosystems. Over their long history, many turtle and tortoise species have evolved a life history characterized by delayed maturity, extended reproductive lives and extreme longevity [3–5]. These co-evolved life-history traits, which served them well in many ecosystems for so long, have rendered them vulnerable to extinction in the face of our rapidly changing world [6].

Turtles and tortoises play important, underappreciated roles in terrestrial and aquatic ecosystems, from seed dispersal to mineral cycling and carbon storage [7]. Populations of turtles and tortoises have been in steep decline for many years [8–13].

Surprisingly, areas of high turtle species richness do not necessarily overlap with terrestrial biodiversity hotspots [14] or areas of tetrapod endemism [15,16]. Freshwater turtles and tortoises occur from 56° N to 42° S latitude, but species richness does not show a high correlation with latitude [15], except at some continent-wide scales, as in North America [17]. Unlike birds, lizards and snakes, turtle species diversity peaks at 25° N latitude rather than near the equator [18]. Freshwater turtle species richness is greatest in the southeastern United States, peaking in the Mobile River basin in Alabama (31° N latitude with 18 species, plus 24 more in the surrounding region) and in the lower Ganges–Brahmaputra River confluence (23° North latitude with 41 species and 9 more in the surrounding region) [15,16,19]. This unusual pattern of turtle species richness is due to climatic, ecological, evolutionary and historical factors, including annual rainfall, mean annual temperature, stream diversity and mean net primary productivity [17,19–21].

The order Testudines — the tortoises, freshwater and marine turtles — is among the most threatened large groups of vertebrates [11,13,22]. Using data from the IUCN (International Union for the Conservation of Nature) Red List and from current extinction assessment risks of turtles by the IUCN Tortoise and Freshwater Turtle Specialist Group [13,22], we assessed the global and regional threats to the group. IUCN's Red List comprises threat categories from Least Concern to Extinct [13]; species considered Vulnerable, Endangered or Critically Endangered are considered 'Threatened' in this review. Of the 360 currently recognized species in14 families, 187 (51.9%) are considered Threatened by IUCN Red List criteria (Figure 1) [13]. Of these, 127 species of the total 360 (35.3%) are Endangered or Critically Endangered. Seven species and ten taxa of chelonians have gone extinct in the past 280 years [11,22]. Three of these (Viesca Mud Turtle, *Kinosternon hirtipes megacephalum*; Seychelles Mud Turtle, *Pelusios castaneus seychellensis*; and Pinta Giant Tortoise, *Chelonoidis abingdonii*) have disappeared in the past several decades. If turtle extinctions continue, we face the imminent loss of a key component of Earth's biodiversity [7].

We review causes of recent precipitous declines in the world's turtle and tortoise populations and compare patterns of species occurrence to extinction risk. Human activities have increased the risk of extinction even in many global biodiversity hotspots that tortoises and freshwater turtles inhabit [14,16,23]. We hypothesize the expected regions and the causes of potential extinction through this century. In doing so, we enumerate threats and describe ways in which their impacts can be mitigated.

Factors Driving Extinction Risk

The main threats facing turtles and tortoises in the early 21st century are habitat loss and degradation, over-collection of turtles and their eggs for food consumption and the international pet trade, as well as over-collection for the trade in traditional medicines made from turtle parts [8–11,24]. Extinction risks vary by geographic region. In Asia, the collection of wild turtles for traditional medicine and food has long been a threat [8,25–27]; in recent years the burgeoning pet trade has also put enormous pressure on many of the same species. The proportion of threatened species of turtles in Asia is significantly higher than expected based on that region's species richness [13]. In Africa, habitat loss and subsistence consumption remain the main threats [28]. In North, Central and South America, extinction risk is primarily from habitat loss or degradation, but commercial collection for the international pet and consumption trade is also a serious problem [29–32].

The main threat of extinction for 80% of those 25 species is commercial or subsistence exploitation. Habitat loss, degradation and fragmentation also affect 80% of these 25 species and comprise the top threat for five species which are restricted to small fragmented or remnant habitat. Table 1 lists the primary threats driving the 25 most endangered chelonian species toward extinction (based on [11]).

Habitat Loss and Degradation

Habitat loss is the leading threat to global biodiversity and to the survival of many chelonian taxa. Habitat loss includes the conversion of habitat for agriculture [33], wetland loss due to degradation and desertification [34], river degradation or diversion due to hydropower projects [26], and landscape fragmentation associated with human population pressure [35].

Forest fragmentation is a form of habitat degradation that can lead to the extirpation of resident species. Because 70% of the world's remaining forest now lies within one kilometer of a forest edge [35], the extent and the impact of habitat fragmentation are profound. Tortoises and turtles and other small animals that occupy mid trophic levels have suffered greatly from forest loss [36]. Populations of the Critically Endangered Dahl's Toad-headed Turtle (*Mesoclemmys dahli*) in the tropical dry forest of Colombia, for example, have become isolated by fragmentation and land conversion to cattle ranching, reducing their effective breeding population size and genetic variability [37]. Small, fragmented populations of Gopher Tortoises (*Gopherus polyphemus*) have reduced hatching success and also reproductive problems attributed to low genetic diversity and inbreeding depression [38].

The leading cause of terrestrial habitat destruction is commercial agriculture, but logging and livestock ranching are also major contributors [39]. In southwestern South Africa, anthropogenic land transformation has destroyed >90% of Geometric Tortoise (*Psammobates geometricus*) habitat [40]. Habitat destruction also played a role in the recent elevation of the status of the Speckled Padloper (*Chersobius signatus*) to Endangered [41]. The spread of towns and cities also increases distances between populations, exposing dispersing and nesting turtles to mortality via road deaths and predators [42].

Because such a high percentage of turtle species are aquatic or semi-aquatic, water quality is a key factor in turtle conservation [43]. The only habitat of the Flattened Musk Turtle (*Sternotherus depressus*) in Alabama are clear-running larger streams with rock-strewn bottoms and healthy mollusk populations. These streams have been degraded by siltation from coal mining, sewage runoff and river impoundments. Only about 7% of the species' historic habitat remains [44], and populations have declined precipitously [11]. Siltation and sand mining [45] have also taken a heavy toll on populations of Asian river turtles of the genus *Batagur* [46]. South American river turtles are also threatened by nesting habitat destruction due to sand mining and dam construction (*e.g.*, Magdalena River Turtle, *Podocnemis lewyana*) [47,48]. In the southeastern United States,

Figure 1. Some of the world's most threatened turtle and tortoise species.
Top (left to right): Painted Terrapin (*Batagur borneoensis*; photo: Gerald Kuchling); Golden Coin Turtle (*Cuora trifasciata*; photo: Gong Shiping); Yangtze Giant Softshell Turtle (*Rafetus swinhoei*; photo: Gerald Kuchling). Middle (left to right): Radiated Tortoise (*Astrochelys radiata*; photo: Craig Stanford); Indochinese Box Turtle (*Cuora galbinifrons*; photo: Craig Stanford); Ploughshare Tortoise (*Astrochelys yniphora*; photo: Turtle Conservancy). Bottom (left to right): Dahl's Toad-headed Turtle (*Mesoclemmys dahli*; photo: Luis Rojas), Bellinger River Sawshelled Turtle (*Myuchelys georgesi*; photo: Arthur Georges); Geometric Tortoise (*Psammobates geometricus*; photo: Turtle Conservancy).

Map Turtles (*Graptemys* spp.) are highly vulnerable to habitat alteration through changes to the natural hydrology and water quality resulting from dams, siltation and pollution [49,50].

Dam construction harms turtle populations by disrupting gene flow, through habitat deterioration (especially of nesting sites) and by interrupting migratory routes [51,52]. Channelization of rivers and shoreline hardening may eliminate nesting and basking areas and alter the hydrodynamic processes that maintain critical nesting habitat [53]. At least 48% of the global river volume has been altered by flow regulation or fragmentation by impoundment structures [54]. Removal of exposed logs and snags to promote recreational boating eliminates critical basking sites and prey habitat [55]. In Australia, aquatic turtles are impacted by water impoundment and human-altered seasonal flooding cycles and timing, intensity and duration of episodic environmental flows [56,57].

The long lifespan of turtles makes them vulnerable to pollutants that accumulate in ecosystems over time. Species that feed at high trophic levels are highly vulnerable to pollutants such as mercury [58,59]. Turtles also lie on or bury into underwater substrates, especially during their winter dormancy called 'brumation', where toxins such as polychlorinated biphenyls (PCBs) and heavy metals accumulate [60]. The incidence and severity of shell anomalies in adult Northern Map Turtles (*Graptemys geographica*) in Pennsylvania corresponded to a growth period during which they were likely to have been exposed to the waste products of coal mining and to high egg incubation temperatures in those waste products [61]. Eggs of female Red-eared Sliders (*Trachemys scripta elegans*) from coal ash-contaminated sites that were incubated in uncontaminated soil still exhibited lower embryo survivorship than did eggs from uncontaminated sites [62]. Harmful algal blooms are a threat to marine ecosystems [63] and marine turtles [64]. Microplastic pollution has also emerged as a threat to both freshwater and marine turtles [65].

In early 2008, Murray River Turtles (*Emydura macquarii*) infested with a parasitic Australian tubeworm were reported at the mouth of the Murray River in South Australia, and reported cases spread upstream until 2011 [66]. In February 2015, a novel virus infecting the Bellinger River Snapping Turtle (*Myuchelys georgesi*) in New South Wales, Australia caused the extirpation of nearly all adults in less than one month [67,68].

Renewable energy development has a large impact on habitat for several turtle species, especially Desert Tortoises (*Gopherus*

Table 1. Relative extinction threats for some of the world's rarest turtles and tortoises.

	Exploitation for trade (pets, food, medicine)	Exploitation for local egg and meat consumption	Habitat loss, degradation and fragmentation	Disease	Climate change
Rafetus swinhoei	30	40	30		
Astrochelys yniphora	90		10		
Cuora yunnanensis	40	10	50		
Batagur baska	50	40	10		
Batagur trivittata	20	80			
Cuora zhoui	70	30			
Cuora mccordi	60	10	30		
Psammobates geometricus			70		30
Cuora aurocapitata	60	10	30		
Mesoclemmys dahli			100		
Cyclanorbis elegans		80	20		
Cuora trifasciata	70	10	20		
Geochelone platynota	80	10	10		
Chelodina mccordi	80	10	10		
Chitra chitra	30	40	30		
Myuchelys georgesi			40	60	
Mauremys annamensis	60	10	30		
Dermatemys mawii	40	60			
Erymnochelys madagascariensis	10	90			
Batagur affinis	20	60	20		
Batagur kachuga	20	60	20		
Leucocephalon yuwonoi	50	30	20		
Pseudemydura umbrina			80		20
Mesoclemmys hogei	10	10	80		
Siebenrockiella leytensis	70	10	20		
Frequency as main threat	**11 (44%)**	**8 (32%)**	**5 (20%)**	**1 (4%)**	**-**
Weight (% of total)	**38.4%**	**26.0%**	**31.2%**	**2.4%**	**2%**

Estimated percentage involvement of threats driving the world's 25 most endangered tortoises and freshwater turtles toward extinction (total for each species = 100%). Estimates based on information provided in TCC (2018) species accounts.

spp.) in the United States [69]. Utility-scale solar and wind facilities have footprints often measured in square kilometers, with impacts on wildlife like turtles that are not yet fully understood [70,71]. A very different kind of habitat degradation is occurring on nesting beaches. Beachfront lighting has been demonstrated to disrupt nest site selection in female marine turtles and the sea-finding orientation of hatchlings to the ocean [72,73]. The effects of artificial lighting on freshwater or terrestrial turtles are unknown [74].

Consumption of Tortoises and Turtles and Their Eggs

Humans have consumed the meat of turtles and tortoises for at least 400,000 years [12,75], and they remain widely exploited. The extinctions of five species of Galapagos Tortoises (*Chelonoidis* spp.) in the Pacific region [76,77] and of five large tortoise species (*Cylindraspis* spp.) from the Mascarene Islands from the 17^{th} to 19^{th} centuries [78] were clearly due to intense collection by crews of passing ships. American whaling ships alone collected more than 13,000 giant tortoises from the Galapagos Island between 1831 and 1868 [78]. Tens of thousands more were taken from Aldabra Atoll in the Indian Ocean, although the population rebounded after collection was halted in the late 19^{th} century [79,80].

In the United States, Diamondback Terrapins (*Malaclemys terrapin*) were harvested to make turtle soup in the late 19^{th} and early 20^{th} centuries [81,82]. The extirpation of European Pond Turtles (*Emys orbicularis*) from most of Central Europe was caused by overharvesting [83]. Madagascar Big-headed Turtles (*Erymnochelys madagascariensis*) were brought to the edge of extinction mainly by exploitation of adults and their eggs by local consumers; commercial collection was never an important factor [84,85].

Marine and freshwater turtles are also heavily exploited for their eggs. Large-bodied riverine turtles of the South American genus *Podocnemis* were historically an important part of the diets of indigenous and colonial people [86]. While legally protected, they are still hunted intensively for their meat and eggs [87], especially nesting females [88–90]. This commercial overexploitation for meat has drastically reduced populations in parts of their range. In some areas where nesting beaches have been protected millions of hatchlings have been released and some local populations are recovering [91]. Even smaller-bodied species such as the Colombian Slider (*Trachemys callirostris*) are heavily exploited for meat and eggs [92]. Likewise, populations of the Pig-nosed Turtle (*Carettochelys insculpta*) have declined by more than 50% due to over-harvesting of eggs and adults by indigenous people in Papua New Guinea [93].

Despite legal protections, all seven marine turtle species have suffered from egg exploitation. While many populations are stable or recovering, others have been extirpated or are imperiled (*e.g*. [94], for eastern Pacific Leatherbacks, *Dermochelys coriacea*). It remains legal in some nations to hunt endangered marine turtles and to collect their eggs [95]. An estimated 42,000 marine turtles were killed legally in 2013 and more than two million were taken legally since 1980 [96]. Marine turtle populations are increasing in many areas and have shown a capacity to recover from intensive depredations in the past [97]. Nest predation by humans and other animals, especially invasive and/or subsidized predators [98–100], is, however, a continuing major problem.

Invasive Species

Invasive animal and plant species have had a severe impact on many wild turtle and tortoise populations as resource competitors, predators and parasites. Predation has impacted many turtle populations; some predators occur at high population densities supported in part by byproducts of agricultural or urban development [101]. The introduced European Red Fox (*Vulpes vulpes*) has devastated native Australian turtle populations. In the Murray River, egg mortality has increased to over 93% [102,103], which may be driving the disappearance of previously common species [57,104]. Predation rates of Diamondback Terrapin nests by mammalian predators are extremely high [105,106]. Rapid range expansion by Pied Crows (*Parvis albus*) [107], assisted by human development, has led to intense predation on several South African tortoise species [108]. Likewise, Common Ravens (*Corvus corax*) prey heavily on Mojave Desert Tortoises (*Gopherus agassizii*) in the southwestern United States [101]. Also, non-native turtles can directly harm native turtle populations. The release of the ubiquitous Red-eared Slider (*Trachemys scripta elegans*) into New World aquatic ecosystems threatens native *Trachemys* species through competition for food and basking sites, and by hybridization [109,110].

Introductions of exotic invasive plants, especially grasses, impact habitats of many turtle species (e.g. *Phragmites* for Diamondback Terrapins) [111]. Invasive plants, along with climate change, have exacerbated the frequency and intensity of fires that impact terrestrial turtles [112]. Fires have severely harmed populations of Desert Tortoises (*Gopherus* spp.) [69,112], Gopher Tortoises (*Gopherus polyphemus*) [113], Chaco Tortoises (*Chelonoidis chilensis*) [114], Hermann's Tortoises (*Testudo hermanni*) [115,116], Spur-thighed Tortoises (*Testudo graeca*) [117], Leopard Tortoises (*Stigmochelys pardalis*) [118], Ploughshare Tortoises (*Astrochelys yniphora*) [119], Radiated Tortoises (*Astrochelys radiata*) [120], Geometric Tortoises (*Psammobates geometricus*) [121], and Box Turtles (*Terrapene* spp.) [122,123].

Infectious diseases caused by bacteria (e.g., *Mycoplasma*) [124] and viruses (e.g., herpes [125] and ranaviruses [126]) seem to be on the rise and have caused major die-offs in turtle populations. Their increased disease transmission has been linked to human activities [127].

Collection for Pet Trade and Medicinal Use

Pet owners have long been fascinated by turtles and tortoises and many species are collected globally for the pet trade. Populations are under intense threat from the pet trade in Asia, where a growing affluence has fueled an appetite for turtles as pets, with rare species commanding astronomical prices. Individuals of some species of *Cuora*, for example, are offered for sale at prices in the tens of thousands of US dollars [128]. Millions of tortoises and freshwater turtles have been exported from North America, Europe and Africa as well [129]. Although many species are now captive-bred to supply the trade and are easily available via the internet [130] or pet shops, vast numbers are still captured in the wild [131] and some are threatened with extinction as a result, such as the African Spurred Tortoise (*Centrochelys sulcata*) in the African Sahel [132,133].

In Madagascar, the Ploughshare Tortoise or Angonoka (*Astrochelys yniphora*) has been collected to the brink of extinction and is likely the world's most endangered tortoise [11,118,134,135]. It has seldom been bred outside Madagascar, and as its population has declined, its value on the black market has increased. Some captive-bred animals have been reintroduced, but many of those have subsequently been poached. Despite its legally protected status, Ploughshares are regularly offered for sale on the internet for high prices and they continue to be smuggled from Madagascar via trading hubs in Southeast Asia [118,136,137]. Recently, nearly 11,000 Critically Endangered Radiated Tortoises (*Astrochelys radiata*) were confiscated from a house in southern Madagascar [138]. Six months later, approximately 7,000 more were confiscated. Most were likely to be smuggled to Asia for the international pet trade, with the largest animals destined for the domestic food market.

The 'laundering' of live tortoises and freshwater turtles is widely practiced to facilitate the illegal and legal pet trade. If a Radiated Tortoise is smuggled from Madagascar to Thailand, it becomes a non-native species upon arrival and is not subject to the laws protecting native Thai wildlife [139]. The tortoise can then be sold legally and will often be falsely advertised as a captive-bred animal rather than an imported one. Range countries should be encouraged to strengthen legislation and law enforcement to close this legal loophole. Pancake Tortoises (*Malacochersus tornieri*) that were poached in Tanzania were usually smuggled to other countries in Africa, from where they could be legally shipped to the rest of the world [140]. The hunter who collected the animals in Tanzania earned as little as US$0.05 per animal, but by the time the tortoise reached the international pet trade, its market value increased to hundreds of U.S. dollars. In addition to the pet trade, some species, especially in Asia, are highly sought after for folk medicinal value. Asian Box Turtles of the genus *Cuora*, especially the Chinese Three-striped Box Turtle (*Cuora trifasciata*), are also collected and captive bred for supposed medicinal value [11,141]. An estimated 1500 turtle farms in southern China produce hundreds of millions of turtles annually to supply food and medicinal markets [142–144]. Some of these farms also breed highly valued pet species and put added pressure on wild populations in their search for more breeding stock. Pet expositions in Asia routinely feature threatened species that were taken from the wild in North America, Latin America and Africa [145].

Climate Change

Our understanding of the impact of climate change on the future of turtles and tortoises is still emerging. Due largely to their long life-spans, declines in turtles that correlate with climate change have been harder to detect than in, for instance, amphibians [24]. Recent studies have suggested that substantial loss of habitat is inevitable, but climate change is impacting various regions differently. In South Africa, drought frequency is expected to increase in some regions, which lowers tortoise egg production in at least some species, such as the Speckled Padloper (*Chersobius signatus*) [146]. The most likely direct impact of climate change related to reduced rainfall may affect the Western Swamp Turtle (*Pseudemydura umbrina*) in southwestern Australia, the only self-sustaining population of which persists in a tiny and highly fragmented ephemeral clay swamp landscape [147]. Some juveniles have been translocated, approximately 250 km outside the species' known distribution, where climate modeling suggested that the new habitat may become more amenable to the released turtles due to climate change [148,149].

Climate change predictions differ regionally. The American Southwest and northern Mexico are forecast to be strongly impacted by increasing aridity. An 88% habitat loss for the Mojave Desert Tortoise in its Sonoran Desert habitat and a 66% habitat loss in its Mojave Desert habitat, both within Joshua Tree National Park, have been predicted for the coming decades [150]. Arid zone species are adapted to extended drought, but the extremes produced by a changing climate may be more than populations can withstand. Large Amazon River Turtles (*Podocnemis* spp.) require dependable river flow cycles to expose sand banks for successful nesting. At one Brazilian site increased river flooding has reduced the time of sandbank exposure during the dry season by an average of 15 days per decade over the last 45 years [151]. Should this trend continue, successful nesting during wet years could be eliminated. Ocean temperature changes and acidification bleach coral reefs, which in turn impact reef-dependent species on which marine turtles feed [152,153]. Furthermore, sea level rise threatens to eliminate suitable nesting sites for marine and estuarine turtles [154,155].

Rising seas in future decades will also inundate low-lying coastal sections of habitat for many freshwater species that are endemic to river drainages. In the Map Turtle and Sawback genus *Graptemys*, a 5-meter rise over the next century would eliminate the habitat of the densest populations of the Yellow-blotched Sawback (*G. flavimaculata*) in the Pascagoula River of southeastern Mississippi, as well as extensive coastal populations of five other Map Turtle and Sawback species [49].

One of the potentially gravest effects of climate change is on incubation temperatures of turtle and tortoise eggs. The sex ratio of egg clutches of many turtle species is determined by temperature during the middle third of incubation; higher temperatures usually produce mainly females [156–160]. Increased substrate temperatures at nesting sites therefore have the potential to skew sex ratios [161,162], thereby reducing population size and genetic diversity in the population. Sex ratio shifts have already been inferred for Hawksbill Turtles (*Eretmochelys imbricata*) [163] and Green Turtles (*Chelonia mydas*) [164]. Loggerhead Turtle (*Caretta caretta*) populations that nest in the southernmost latitudes of the United States are already female-biased compared to those nesting at higher latitudes [165]. Similarly, the primary sex ratio in northern Great Barrier Reef populations of Green Turtles (*Chelonia mydas*) are 87–100% female, while those in cooler-temperature southern populations are 65–69% female [163].

In turtle conservation, as with so many other groups, climate change is occurring as the background to more imminent anthropogenic threats. In the long term, climatic issues will shift the baseline of habitat suitability in ways that we are only starting to understand.

Addressing Extinction Threats

The combined effects of habitat loss and degradation, consumption and use of the animals and their eggs, invasive species impacts, and climate change are bringing many of the world's tortoises and turtles to the brink of extinction [13], and more than 100 species are now severely threatened (Figures 2 and 3). Many other species are nearly extinct in the wild and are being bred in captivity, but there is no protected habitat remaining to which they can be securely reintroduced. It will be a daunting challenge for conservationists to preserve turtle and tortoise biodiversity through the 21st century and beyond. The largest vertebrates tend to receive the most attention from both conservationists and the public. Iconic species such as Galapagos Giant Tortoises, Aldabra Giant Tortoises, Mojave Desert Tortoises and marine turtles have been the recipients of relatively robust funding, time and energy aimed at protecting remaining populations. Despite this attention, the Mojave Desert Tortoise, arguably the best studied endangered tortoise species [166], is declining throughout its range despite being federally protected since 1990 [167].

Habitat Protection

Preventing turtle extinctions in the 21st century will require protecting remaining habitat, especially hotspots of species diversity. Sixteen areas of high turtle biodiversity that were surveyed comprised 262 species, or 83% of the 315 recognized turtle species at the time of the study [16], and nearly half (47%) of those species were endemic to those 16 hotspots. Although these numbers have not been recalculated for the 41 additional species now recognized [22], that study indicated that protecting 16 hotspots, which represent approximately 24 million km^2, or about 16.0% of the land surface, would protect the majority of turtles on Earth.

Overall, 342 taxa (79%) occur in those 16 hotspots, which represent approximately 24 million km^2, or about 16.0% of Earth's land surface. Less than 10.4 million km^2 (7%) remain covered by original, non-degraded habitat. Because of the high fecundity and longevity of some turtle species, maintaining and protecting limited nesting habitat may provide enough hatchlings for release throughout a species' distribution (Figure 4) [103]. Habitat loss is an enormous problem for turtles and tortoises, as for all of Earth's biodiversity. The effects can be mitigated if we are able to protect turtle biodiversity hotspots, particularly those with critical nesting habitat.

The Culture of Turtle and Egg Consumption

Lowering the consumption of turtles and their eggs is a crucial conservation goal. It was estimated that more than 25 tons of live turtles were exported weekly from Sumatra to Hong Kong

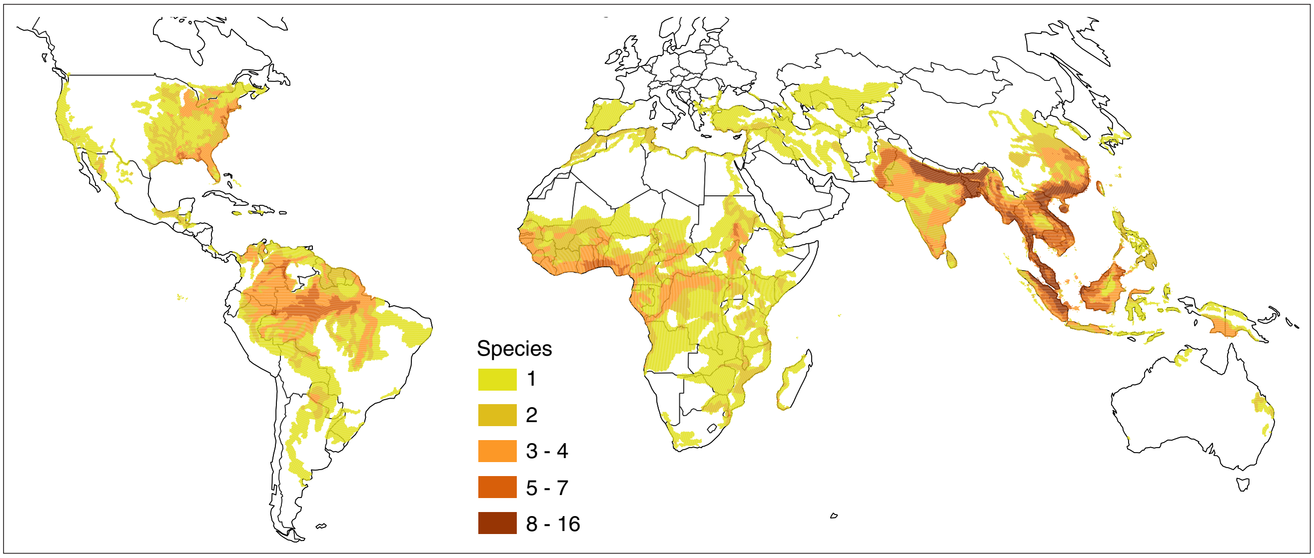

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Figure 2. Map of threatened turtle and tortoise diversity.
Global species richness of tortoises and freshwater turtles threatened with extinction, showing turtle biodiversity hotspots in Southeastern United States, Gangetic Plains of South Asia, and coastal Southeast Asia. IUCN Red List categories CR, EN, and VU [22].

and China in the late 1990s [168]. In a study of wildlife in the food markets of southern China, 28 species of turtles were available for sale (29% of all vertebrate species observed in markets), including eight Vulnerable, 12 Endangered, and one Critically Endangered species [169].

Turtle farming supplies millions of animals to the food industry in Asia; turtle farms in China and Southeast Asia have been highly successful at turning East Asian softshell turtles (primarily the Chinese Softshell, *Pelodiscus sinensis*) into a commercially valuable commodity [142,143]. It appears, however, that many farms augment their breeding stock by obtaining wild turtles legally or illegally and thereby increase the human demand for turtles [142]. This suggests that turtle farms may intensify rather than lessen collecting pressure on wild populations. In addition, escaped farm turtles pose an imminent genetic and ecological threat to native wild populations [143].

Egg poaching accounts for dramatic declines in some marine turtle populations, as well as declines in large river turtles in Asia (e.g. *Batagur* spp.) and South America (e.g., *Podocnemis* spp.) [8]. Some populations have been protected on their nesting beaches through agreements with local communities that allow controlled harvesting of eggs. In Costa Rica, egg collecting from Olive Ridley Turtles (*Lepidochelys olivacea*) [170] has been legalized and regulated to strike a balance between the demands of local communities and conservationists. Conservationists recommended allowing the collection of earliest-laid egg clutches, with strict protection of the second and third nesting cycles to mitigate the impact on populations while providing an incentive for local people to protect the nesting beaches [170,171]. The plan has been criticized for perpetuating a culture of egg poaching that impacts other, unprotected wildlife. As an extinction threat, however, subsistence collection is dwarfed by commercial egg harvesting [48]. While turtle meat and egg consumption may have declined for some species, they remain a major problem for others and in some geographic regions.

Both marine and freshwater turtles are caught and killed as bycatch in fishing nets; Turtle Exclusion Devices (TEDs) have been implemented with success on some marine fishing grounds [172]. Lethal bycatch of Diamondback Terrapins in crab traps in estuaries along the East Coast of the United States has had catastrophic effects [173,174]. In one study, an estimated 15-78% of local terrapin populations were lost annually to crab traps in Maryland [172]. A number of bycatch reduction devices (BRDs) have been designed to reduce this mortality [175,176], but laws regarding their structure and use are unevenly implemented. Research has only recently begun on the effects of fisheries bycatch on freshwater turtle populations [177–180].

The Pet Trade and Captive Breeding for Conservation

The international pet trade threatens many turtle and tortoise species. In theory, captive-bred populations could reduce pressure on the unsustainable harvest of some turtle species from the wild to supply the pet trade [128]. There are notable cases of captive breeding success with threatened species. Because of their potential longevity and since many species can be captive-bred, assurance colonies for potential reintroductions can be created for chelonian species that are Critically Endangered or extinct in the wild [181]. The Española Giant Galapagos Tortoise (*Chelonoidis hoodensis*) was rescued from the brink of extinction by bringing together the last 15 individuals in captivity and breeding them, followed by the release of head-started progeny [182]. In Australia, the Western Swamp Turtle was rescued from near-extinction by captive breeding and reintroductions [146]. Burmese Star Tortoises (*Geochelone platynota*) were functionally extinct in the wild in Myanmar, but more than 20,000 have been bred in captivity and animals are now being successfully released into protected areas within their former range [183]. Bolson Tortoises

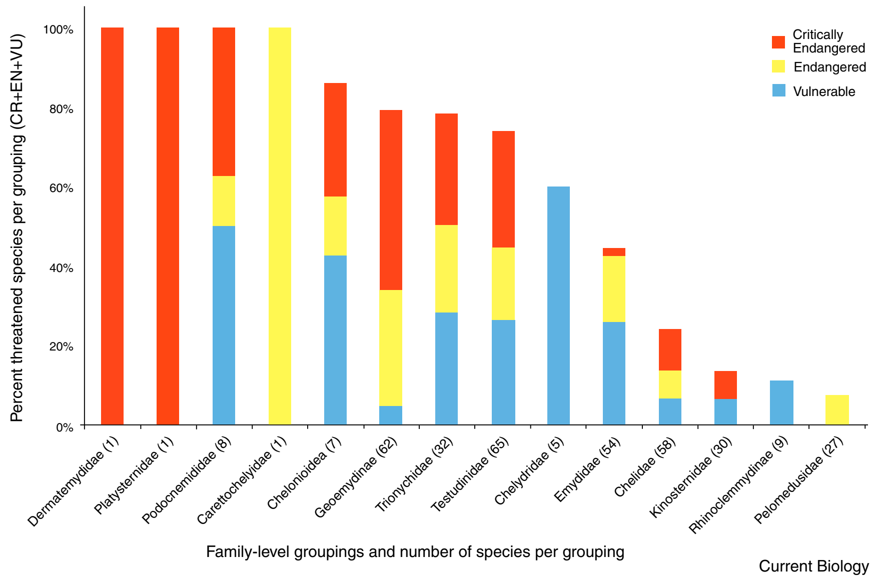

Figure 3. Threat levels in turtle and tortoise families.
Percentage of turtle and tortoise families (with number of species per family) and species threatened with extinction (IUCN Red List categories CR, EN, and VU). The family Geoemydidae analyzed by its two component subfamilies, Geoemydinae and Rhinoclemmydinae. Adapted from [13].

(*Gopherus flavomarginatus*) are being bred in captivity with the eventual goal of reintroducing the species to its former Pleistocene distribution in New Mexico, United States [184].

Whether captive breeding has been effective as a conservation tool over a wider range of turtle and tortoise species is unknown. The more threatened a species becomes, the higher its monetary value, driving the collection of the last remaining wild populations [118,135,136]. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) regulates the commerce of many turtles and tortoises by restricting international transport of those species deemed threatened enough to be placed on the CITES Appendices, though there are loopholes. Existing laws must be enforced, and new laws must be enacted to close existing legal loopholes, along with increasing public awareness of the problem.

Releasing captive bred tortoises and turtles into the wild involves its own set of challenges. Natural habitat must exist and be protected to prevent poaching of released animals. At least one species not yet recorded in the wild (*Cuora zhoui*) is being bred in captivity in Europe, but unless secure habitat is located, reintroduction is unlikely [11]. Local communities, including former poachers, can be educated about the release and perhaps involved in re-introducing the species. Captive breeding necessitates a substantial investment of time, energy and funding. A captive population may need to be genetically managed for many years in hope of an appropriate release location becoming available.

For some species, if *in situ* conservation efforts fail, captive breeding and assurance colonies can prevent extinction. Hatchling turtles can be reared in captivity until they reach a size that reduces predation risk [185,186]. Existing head-starting programs already release thousands of juveniles into the wild [180,187]. Especially when accompanied by community involvement to allow local people to be stakeholders in the conservation effort, head-starting can be a powerful tool [188]. Marine and freshwater turtle nesting protection and hatchling release projects have been undertaken in many regions, in which egg clutches are relocated from threatened beaches to beach hatcheries. This has led to increases in some populations.

There are concerns about egg hatcheries: skewed sex ratios, low hatching success, reduced hatchling viability [189–191] and altered hatchling size and condition [192,193]. One study showed that head-starting disrupts the natural migratory behavior of Giant South American River Turtles (*Podocnemis expansa*) [194]. It may also compromise their population genetics if some nest areas are better protected than others [103], although the longevity and high fecundity of many species may offset genetic issues [195]. Head-starting has been credited with increasing recruitment for populations of some species (e.g., Kemp's Ridley, *Lepidochelys kempi* [196]; Diamondback Terrapins [53]), but follow-up studies are needed. The long-term success of head-starting has not been widely evaluated quantitatively; deterministic and stochastic modeling suggest it will not save declining populations (e.g., [197]; [6] for marine turtles; [48,67,198] for freshwater turtles).

Innovative Conservation Techniques

The goal of turtle conservation is to ensure that there are long-term viable populations for every living species. To succeed, data on ecology, demography, habitat management, genetics and husbandry need to be incorporated into management plans for each species. Changes in land use, increasing human development and climate change variables must be included in management plans. The metrics of conservation success are different for tortoises and turtles than they are for most other animals. Their delayed sexual maturity, extended fertility and longevity means that conservationists may need many decades to determine whether a demographically healthy, age-diverse population has been successfully protected or reintroduced (see [181] for a successful example and [199,200] for unsuccessful ones).

Technology has long assisted conservationists in monitoring chelonian populations and their vulnerability to extinction risks [201]. Radio telemetry has been critical to turtle research in the field. GPS-linked tracking devices enable researchers to obtain information on where animals spend their lives away from nesting beaches [50]. Passive integrated transponder tags enable biologists to identify individual turtles through time [202], which is essential for monitoring demographic parameters of wild populations. Soft release methodologies, such as penning, increase survival and site fidelity of individuals in reintroduced populations [203].

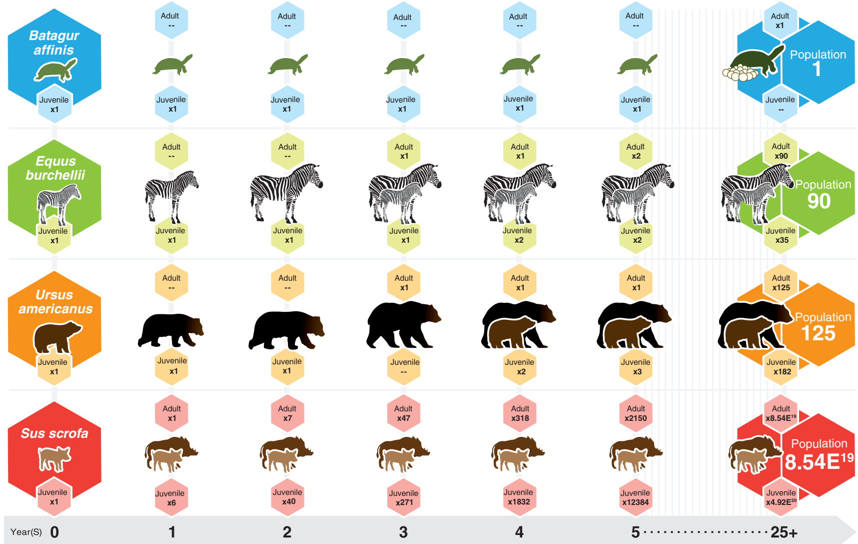

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Figure 4. The low lifetime reproductive potential of turtles compared to selected other vertebrates.
Despite their ability to produce many eggs per clutch, many turtle species have a lower reproductive potential than mammals that bear only one or two offspring at a time.

Side-scan sonar is a new tool in turtle conservation that allows field biologists to see the underwater structure of ponds, streams and rivers [204]. It can even image turtles themselves as they swim or walk deep underwater. This technique allows biologists to evaluate habitat structure and suitability, and to estimate non-invasively the population status of rare species in environments with poor visibility such as blackwater rivers, murky ponds and swamps. Unmanned aerial vehicles (drones) have also added a powerful new tool for surveying and studying wild turtle populations [205,206].

Environmental DNA (eDNA) is a powerful emerging tool that allows conservation biologists to detect cryptic or rare species in aquatic or terrestrial habitats [207–209]. The presence of one individual in a sizable lake can be detected by DNA shed from feces, skin or shells [210]. The use of eDNA has, for example, recently established the presence of a specimen of the nearly extinct Giant Yangtze Softshell Turtle (*Rafetus swinhoei*) in a lake in northern Vietnam [211].

Researchers must engage local communities in conservation efforts. Projects that use trained ‘guardians’ who watch over wild tortoise, freshwater turtle and marine turtle populations also benefit from the funds that ecotourism generates. Partnerships with communities and local governments can be highly effective for *in situ* conservation [187,212,213].

Conclusions

Although the threats to tortoises and freshwater and marine turtles are severe, only one species and three taxa have gone extinct in the past two centuries. At least three species have been rescued from near-extinction. These successes give us reason for hope. However, other turtle taxa are already likely functionally extinct in the wild and may soon disappear without human intervention. Human population growth, increasing ambient temperatures, and associated habitat loss are increasing, as are the burgeoning food and pet trades in Asia and elsewhere. Immediate concerted action is thus required if we are to have any hope of meeting a goal of zero turtle extinctions in coming decades.

The underappreciated roles that turtles and tortoises play in Earth’s ecosystems underscores how declining chelonian diversity represents a substantial loss to ecosystem function [7]. Our review outlines the many threats faced by turtles and tortoises and suggests necessary steps to mitigate and reverse those threats. The goal of all conservationists is to improve the prospects of long-term species survival in healthy ecosystems. Among the most intriguing of Earth’s life forms, turtles and tortoises need urgent conservation attention to avoid catastrophic extinctions in the immediate future.

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This paper is dedicated to the memory of two of our coauthors who passed away late in the publication process: Margaretha Hofmeyr and Peter Pritchard. Their contributions to the conservation biology of turtles and tortoises were enormous, and they will be greatly missed. Disclaimer [required by coauthors who are government employees]: any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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