

Where Have All the Turtles Gone, and Why Does It Matter?

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Of the 356 species of turtles worldwide, approximately 61% are threatened or already extinct. Turtles are among the most threatened of the major groups of vertebrates, in general, more so than birds, mammals, fishes or even the much besieged amphibians. Reasons for the dire situation of turtles worldwide include the familiar list of impacts to other species including habitat destruction, unsustainable overexploitation for pets and food, and climate change (many turtles have environmental sex determination). Two notable characteristics of pre-Anthropocene turtles were their massive population sizes and correspondingly high biomasses, the latter among the highest values (over 855 kilograms per hectare) ever reported for animals. As a result of their numerical dominance, turtles have played important roles as significant bioturbators of soils, infaunal miners of sea floors, dispersers and germination enhancers of seeds, nutrient cyclers, and consumers. The collapse of turtle populations on a global scale has greatly diminished their ecological roles.

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Turtles are so universally recognized by virtually all cultures and age groups that it is easy to see them as merely commonplace animals, even though many are far from common. This prosaic status makes them easy to take for granted or even overlook as important ecosystem components worthy of protection. The word *turtle* applies to all animals with a bony shell and a backbone, whether they are locally referred to as turtles, tortoises, or terrapins (Ernst and Lovich 2009). That such remarkable and familiar animals are considered by many to be ordinary is unfortunate, because no vertebrate animal that has ever lived has possessed the unique architecture of turtles, with their limb girdles encased inside a bony shell. As previous paleontologists have noted, if they were known only from fossils, they would be cause for wonder. Turtles are an ancient group going back over 200 million years (Ernst and Lovich 2009). Their enduring success is due in no small part to a conservative morphology and time-tested adaptations that allowed them to outlive even the dinosaurs, which disappeared over 65 million years ago, when turtles were already an old lineage.

Turtles are struggling to persist in the modern world, and that fact is generally unrecognized or even ignored. Scientists identify 14 living families and many extinct ones. As of 2017, 356 turtle species were recognized worldwide (Turtle Taxonomy Working Group 2017), of which approximately 61% are threatened or have become extinct in modern times. Turtles are arguably the most threatened of the major groups of vertebrates in general and are proportionately more so than birds, mammals, fishes or even the much-besieged and

heavily publicized amphibians (Hoffmann et al. 2010). The vulnerability of turtles, in part, is due to a global focus by conservation programs to prioritize and target areas that protect birds and mammals but do not adequately consider turtle diversity (Roll et al. 2017).

Specific examples of the recent plight of turtles are exemplified by several species worldwide. For example, some turtle species are no longer found in their native habitat and exist only in captivity. One such species, the Yangtze giant softshell turtle (*Rafetus swinhoei*) is reduced to perhaps four surviving individuals, and only one is known to be a female. For the past 8 or more years, she has not produced fertile eggs, despite international efforts to propagate the species, including the use of artificial insemination. Others, such as the beautiful Burmese star tortoise (*Geochelone platynota*) and the less-charismatic western swamp turtle (*Pseudemys umbrina*), Australia's rarest reptile, are among the 25 most endangered turtles in the world (Turtle Conservation Coalition 2018), requiring captive breeding and intensive management to keep them from extinction. The death of "Lonesome George" in 2012, the last purebred Pinta giant tortoise (*Chelonoidis abingdonii*) in the Galápagos Islands, marked the extinction of yet another turtle species (Edwards et al. 2013).

Reasons for the dire situation turtles face worldwide include the familiar litany of impacts to other species (Gibbons et al. 2000) including habitat destruction, unsustainable overexploitation for food and the commercial pet trade, and climate change (many turtles have environmental sex determination). Disease has also contributed to the rapid

decline and near extinction of some turtle species (Spencer et al. 2018). The fate of turtles is especially tragic in light of their distinction as paragons of evolutionary success. They survived everything nature could throw at them from both Earth and outer space (e.g., the asteroid that wiped out the dinosaurs), but will they survive modern humans? Hominids have overused turtles as part of a subsistence diet since the development of Oldowan stone technology in Africa 2.6 million years ago (Turtle Extinctions Working Group 2015). As an example, of the 61 modern (living and extinct since 1500 CE) tortoises plus 60 extinct fossil species that have existed since the beginning of the Pleistocene, 57% (69 of 121) are now extinct. Being slow, terrestrial, and defenseless, tortoises became an easy mark for early, as well as more recent, hominids (White et al. 2010). The exploitation of turtles has been exacerbated in the modern age (e.g., Mali et al. 2014), with many turtle populations increasingly edging toward extinction. Tragically, as some desirable species become rarer, the demand for them increases in the illegal pet trade, accelerating their decline. The collapse of turtle populations on a global scale has greatly diminished their ecological roles as important members of their biotic communities. Our objective is to bring attention to the plight of turtles and identify what we will lose from an ecological perspective as they continue to decline and disappear.

One way to increase recognition of the value of species is to look at the services they provide to an ecosystem, including those increasingly dominated by humans. The perceived functional roles of various organisms in their environments have been topics of great interest to ecologists. Population declines can lead to function loss in ecosystems that may not be immediately apparent. Numerous publications now document the important ecological roles a wide variety of species provide in their environments, but in few have the roles turtles play been examined. In the present article, we review the various functional roles that large populations and diverse communities of turtles provide from an ecological perspective, expanding on an earlier, brief review (Ernst and Lovich 2009). A major goal is to place turtles within the overall context of ecosystem processes and services including energy flow, trophic status, mineral cycling, scavenging, and soil dynamics. Identifying these critical ecological roles is one step toward offering rationales for concerted efforts to conserve these emblematic creatures that have accompanied us into the Anthropocene, a time of extinction and decline for many terrestrial vertebrates (Dirzo et al. 2014).

(The term *Anthropocene* is not formally recognized by the US Geological Survey as a description of geologic time. We use it here informally. The origins of the term are discussed in Zalasiewicz et al. 2008.)

Biomass contributions: Turtles throw their weight around

Biomass is an important measure in ecology, because it reflects the amount of available and stored energy in the plants and animals occupying an ecosystem. High biomass of

a species or group of species within an ecosystem commonly results in a greater impact on ecosystem processes. Many turtle populations make or made significant contributions to the biomass of their environment, as first noted by Iverson (1982). Turtle standing crop biomass is generally very high in comparison with other vertebrates (figure 1), often surpassing that of all other reptiles. Biomass values for turtles are typically at least an order of magnitude higher than those of other reptiles and similar to those of large schools of fish. The high biomass of turtles is related largely to the high population densities they are capable of achieving. For example, two centuries ago, sea turtles were estimated to number in the tens of millions in the Caribbean Sea alone. More recently, their numbers were estimated in the tens of thousands (Jackson et al. 2001). In the last 40 some years alone, various major groups of marine vertebrate populations, including sea turtles, have declined an estimated 22% on average (McCauley et al. 2015), further diminishing their impacts on that ecosystem.

The highest accepted biomass for an aquatic turtle is 877 kilograms per hectare (kg per ha; Congdon et al. 1986) for pond slider turtles (*Trachemys scripta*), a species that can have as many as 2200 individuals per hectare in some habitats (DeGregorio et al. 2012). At a minimum of 583 kg per ha, the Aldabra tortoise (*Aldabrachelys gigantea*) achieves the highest undisputed standing crop biomass for tortoises (Coe et al. 1979). Aquatic species such as the Mexican mud turtle (*Kinosternon integrum*) and the Llanos sideneck turtle (*Podocnemis vogli*) are reported to achieve standing crop biomasses of 2860 kg per ha and 15,450 kg per ha, respectively, although these values represent temporary aggregations or exaggerations (Iverson 1982). Mass nesting *arribadas* of sea turtles are classic examples of temporary aggregations and exceptional concentration of biomass on nesting beaches (Ernst and Lovich 2009). The numbers reported above are truly remarkable biomass figures, surpassing even the maximum value (199 kg per ha) reported by Coe and colleagues (1976) for herds of large herbivores on the African plains! At these historically high densities and biomasses, turtles had a major impact in their ecosystems, especially as consumers but also as prey. Therefore, extirpation or population declines of turtles can result in alteration of ecosystem structure and function as described in the sections below.

Turtles also contribute substantially to secondary productivity in some ecosystems. Estimates of annual biomass production (growth of individuals plus egg production) range from 7.3 kg per ha for a community of three turtle species in southeastern Michigan to 9.7 kg per ha for a community of six turtle species in South Carolina (Congdon and Gibbons 1989). As a consequence of their overall secondary productivity and biomass, turtles have a disproportionate influence on processes in many wetland and terrestrial environments, as described further in the sections below. Even more diverse turtle communities exist in biodiversity hotspots, such as the southeastern United States (Buhlmann et al. 2009), and more research is needed to better understand their aggregate

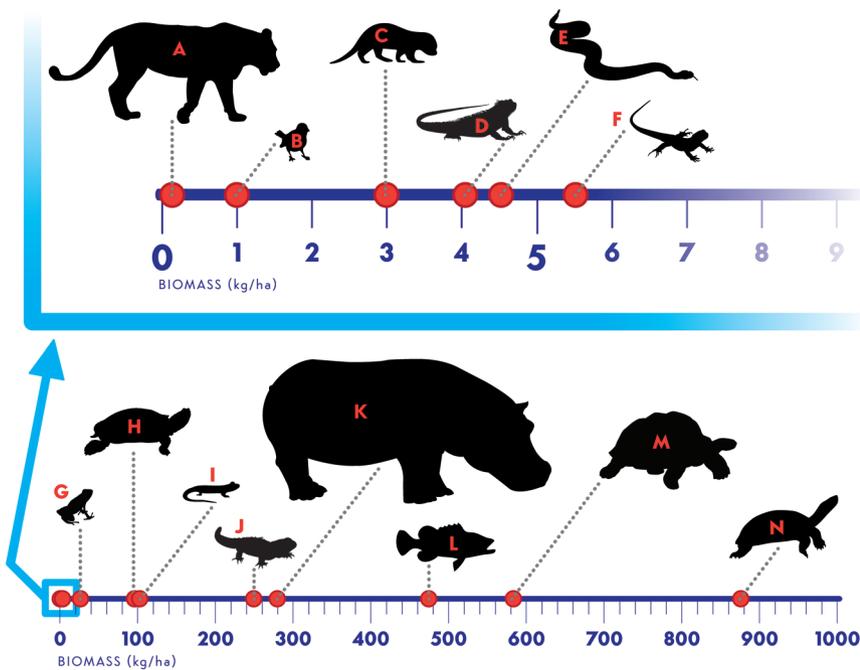


Figure 1. Maximum biomass estimates for several major vertebrate assemblages (represented with generic silhouettes), subdivided into dietary groups, such as herbivorous, omnivorous, and carnivorous species. The top image is an inset displaying biomass estimates that were less than 10 kilograms per hectare (kg per ha) and difficult to display on the bottom image. (a) large carnivorous mammals (0.24 kg per ha), (b) birds (approximately 1.0 kg per ha), (c) small carnivorous mammals (approximately 3.0 kg per ha), (d) herbivorous lizards (4.1 kg per ha), (e) snakes (4.58 kg per ha), (f) carnivorous lizards (5.5 kg per ha), (g) frogs (27.3 kg per ha), (h) carnivorous turtles—e.g., Sonora mud turtle—(100.3 kg per ha), (i) aquatic salamanders (99.3 kg per ha), (j) tuataras (250 kg per ha), (k) large herbivorous mammals (280 kg per ha), (l) fish (477 kg per ha), (m) herbivorous turtles—e.g., Aldabra giant tortoise—(583.5 kg per ha), and (n) omnivorous turtles—e.g., red-eared slider turtle—(877 kg per ha). All estimates are from Iverson (1982), except for omnivorous turtles (Congdon et al. 1986) and aquatic salamanders (Peterman et al. 2008).

biomass contributions and ecological interactions (e.g., Lindeman 2000).

What conditions allow some turtle species to attain such extraordinarily high standing crop biomasses? In a review of the role of desert vertebrates in the ecosystem, Brown (1986) noted several factors that contribute to the diversity and high biomass of desert reptiles. First, habitats that could support only a small number of endothermic, or warm-blooded, birds or mammals can support a much larger population of reptiles, such as turtles. The available data suggest that reptiles are at least an order of magnitude more energetically efficient than endotherms, converting a higher proportion of assimilated energy into biomass and making it available to predators at higher trophic levels (Vitt and Caldwell 2009). Herbivorous turtles may even expend energy at a slower rate for their body mass than some other herbivorous reptiles (Jodice et al. 2006). Second, reptiles can become dormant during long periods of low resource availability. Therefore,

the abundance of some desert reptiles can be partially attributed to low productivity in the desert ecosystem that favors organisms with low metabolic requirements and the ability to become dormant during lean times. Endotherms that lack the ability to remain inactive under adverse conditions must migrate to other areas.

All of the Aldabra tortoise's close relatives (i.e., *Cylindraspis* spp.) were endemic to the Mascarene Islands in the Indian Ocean east of Madagascar and most likely reached high biomasses prior to overexploitation as well (Gerlach et al. 2013). Unfortunately, most of these species have been driven to extinction (Turtle Extinctions Working Group 2015). Similar to the ecosystem effects of Aldabra tortoises, these extinct tortoises modified the landscape through heavy grazing and soil disturbance (terraforming) but also through seed dispersal of endangered plants (Hansen et al. 2008). Without the ecosystem services provided by these tortoise species, many of these island ecosystems have become degraded. The history of tortoises on these and other islands provides a cautionary tale of how important turtles can be in their ecosystems. Because turtles contribute a significant portion of the overall biomass to an ecosystem, turtles are strongly linked to ecosystem health and function through resource subsidies, mineral cycling, top-down food web effects, seed dispersal and germination enhancement, and bioturbation. All of these topics are discussed in the following sections.

Energy flow within and between ecosystems

Production of organic matter in living organisms requires harvesting food resources, and turtles certainly play a role in the energy flow of their immediate and surrounding environment. Because turtle nest predation rates may be 100% in some years (Congdon et al. 2000), eggs provide a significant redistribution of energy and nutrients between aquatic and terrestrial habitats (see Moss 2017), as well as between turtles and their predators (Congdon and Gibbons 1989). The dried contents of turtle eggs are almost entirely protein and lipids (Booth 2003). A detailed example of this energy transfer from marine to terrestrial environments was provided for nesting sea turtles on a beach in Florida (Bouchard and Bjorndal 2000). Loggerhead sea turtles (*Caretta caretta*) deposited 14,305 nests, with an estimated 1.6 million eggs, in a 21-kilometer stretch of beach in 1996.

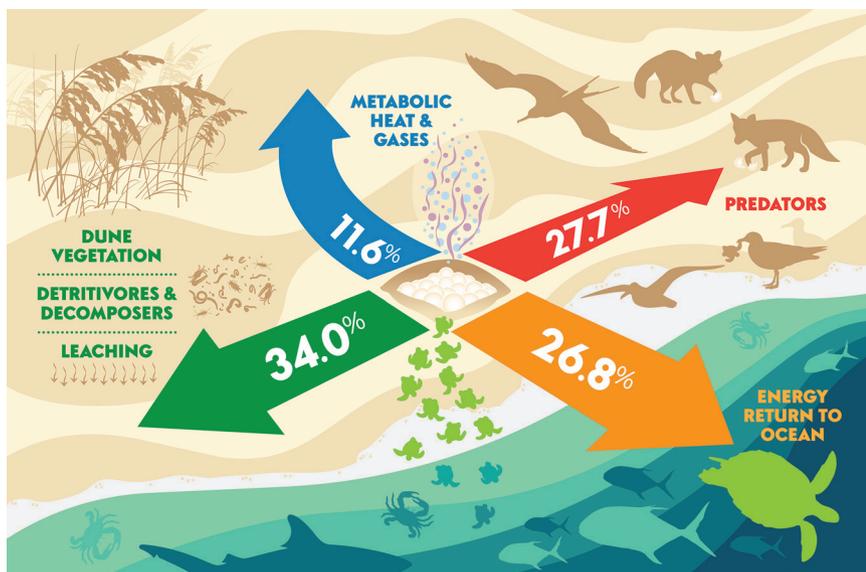


Figure 2. Energy in nutrients transferred from marine to terrestrial environments by nesting sea turtles is now greatly diminished with worldwide reductions in sea turtle populations. This figure shows the projected transfer of energy from 14,305 loggerhead sea turtle (*Caretta caretta*) nests with an estimated 1.6 million eggs on a 21-kilometer stretch of Florida beach in 1996 (Bouchard and Bjorndal 2000). Note that only about one quarter of total energy transferred to beaches returned to the marine environment in hatchlings.

On average, each nest transferred 688 grams (g) of organic matter, 18,724 kilojoules (kJ) of energy, 151 g of lipids, 72 g of nitrogen, and 6.5 g of phosphorus into the nutrient-poor beach environment. Only about 27% of the energy content contained in these nests returned to the ocean as hatchlings, and the remainder stayed onshore (figure 2). In their review, Bouchard and Bjorndal (2000) concluded that the energy and nutrients introduced by turtles in this fashion are comparable to the quantities moved by other cross-ecosystem transport systems involving birds. By introducing nutrients into beach ecosystems, sea turtles may help maintain stable dune systems that are critical to their reproductive success. In another example of nutrient transfer, American beach grass (*Ammophila breviligulata*), which stabilizes dune nesting habitat for turtles, is capable of absorbing nutrients directly from the eggs of diamond-backed terrapin (*Malaclemys terrapin*) nests (Stegman et al. 1988). In addition, nutrients from the eggs in sea turtle nests influence the beach meiofauna, especially nematodes (Diane et al. 2017).

The second reason supporting the importance of turtles in energy flow relates to their role as consumers, particularly as scavengers. Thompson (1993) studied a riverine community of three turtle species in Australia. Making a variety of assumptions on population densities and distribution of the species, he estimated their standing crop biomass as 27.9–279.3 kg per ha. Assuming that their diet is 20% carrion, the energy throughput of turtles was conservatively estimated at between 13.5×10^7 and 13.5×10^8 kJ per day, on the basis of consumption of 430 metric tons

of carrion per day during the summer in his 358,000-ha study area. Additional information on the role of turtles as consumers is summarized in the section on trophic status.

The scavenging value of turtles even has profound importance in the cleanup of rivers polluted by humans (Sinha 1995). The Ganges River in India is badly polluted with, among other things, the partially cremated corpses of humans on the *ghats*, or stairs, along the river. In 1992 in Varanasi alone, officials estimated that 20,000–30,000 human bodies were cremated annually. At that time, the Indian government spent \$32 million building farms to produce scavenging turtles to assist with the elimination of corpses. About 24,000 turtles were raised and released into the Ganges since the program was initiated in 1990 (Anderson 1992). It is estimated that a fully grown turtle can eat about one pound of meat per day. Whether turtles are making a difference is subject to local debate.

Mineral cycling and bioaccumulation

Mineral cycling involves the transfer of life-essential nutrients and elements from the environment to organisms and back to the environment, from birth to death. The high standing crop biomass of some species, coupled with the fact that 82% of the dry mass of some turtles is bone (Sterrett et al. 2015), suggest that they may occupy a prominent position in the mineral cycles of some ecosystems, particularly in those that may be calcium or phosphorus deficient. However, the role of turtles in calcium and phosphorus cycling is virtually unknown.

Radioecological studies with an isotope of strontium (^{90}Sr), a bone-seeking calcium analog, provide a glimpse of the potential role turtles play in the calcium cycle (Hinton and Scott 1990). These researchers found that turtles are similar to other organisms in their ability to concentrate ^{90}Sr , but herbivorous species such as the gopher tortoise (*Gopherus polyphemus*) may accumulate higher concentrations than other turtles do because of their trophic position. This is because levels of ^{90}Sr tend to be higher in vegetation than at higher trophic levels occupied by omnivorous or carnivorous turtles. However, a significant difference between turtles and other aquatic organisms is the concentration ratio between the animal and its environment. Concentration ratios are useful for comparing organisms because they normalize for variations in the radionuclide concentration of the environment (e.g., water) and indicate the propensity for a radioisotope to concentrate within an organism. Concentration ratios for turtles are very high

relative to other organisms, showing their propensity to accumulate ^{90}Sr as a calcium analog in the periodic table. High concentration ratios can be associated with low availability of the nutrient element analog (calcium), longevity, high assimilation, long retention time, or some combination thereof. The long lifespan of many turtles (Gibbons 1987), their high percentage of slowly developing bone, and their high assimilation rates make them a potentially important link in the calcium cycle of some ecosystems (Hinton and Scott 1990).

Agassiz's desert tortoises (*Gopherus agassizii*) have been observed to "mine" and eat calcium carbonate deposits at the surface or under a thin layer of excavated overburden. These episodes, known as *geophagy*, have only been observed in sexually mature females during the nesting season, a time when females may experience calcium stress due to egg production (Marlow and Tollestrup 1982). *Osteophagy*, or the consumption of bones, has also been observed in *G. agassizii* and may be similarly related to calcium, phosphorus, or other mineral deficiencies in the diet (Esque and Peters 1994).

A bizarre case of mineral cycling and subsequent disease transmission among tortoises and ungulates in Ethiopia was reported by Mengiste and colleagues (1990). Bovine botulism in southern Africa has long been associated with the consumption of dead tortoises by cattle (Fourie 1946). Mengiste and his colleagues (1990) suggested that soil in the affected area was deficient in phosphorus, forcing cattle to consume dead tortoises as a source of that element, ultimately infecting them with botulism bacteria that originated in the rotting carcasses.

The role of turtles in mineral cycles also makes them excellent environmental indicators for chemicals of concern to human health. Because of the long lives and relatively high trophic position of omnivorous and carnivorous species in aquatic environments, they have the potential to accumulate significant levels of some pollutants (e.g., Hebert et al. 1993) including PCBs, DDT, Mirex, and other toxic compounds, rendering them unfit for human consumption. North American turtles have been shown to be effective for monitoring mercury contamination (Golet and Haines 2001) and even radioactivity in aquatic systems (Hinton and Scott 1990).

Trophic status: Turtles as predators and prey

The trophic position of an organism in a food web can have important direct effects on community structure through top-down or bottom-up cascades. As a group, turtles occupy trophic positions as herbivores, carnivores, and omnivores and play important, even dominant, roles (Hastings et al. 2014) in their communities, sometimes as a top predator (Fukumori et al. 2016). Perusal of the feeding habits of the 257 turtle species recognized at the time by Ernst and Barbour (1989) shows that the natural diets of about 180 species are known with some degree of confidence. Of these, roughly a third each are omnivores, carnivores, and herbivores. Some species are highly specialized, and others are more opportunistic, each playing a role in their trophic

niche. The leatherback sea turtle (*Dermochelys coriacea*) feeds almost exclusively on jellyfish. This is a niche occupied by few other large marine predators, with the exception of the ocean sunfish (*Mola mola*; Ernst and Lovich 2009). The hawksbill turtle (*Eretmochelys imbricata*) also has a specialized diet, feeding almost exclusively on sponges (Meylan 1988). In contrast, many other species, such as adult slider turtles, are opportunistic omnivores with a very catholic diet (Parmenter and Avery 1990).

In turn, turtles and their eggs are prey to an incredibly diverse array of predators including both invertebrates and vertebrates (see Ernst and Lovich 2009 for numerous examples). Evidence of turtles as prey species dates to at least the lower Cretaceous of Australia, when prehistoric ichthyosaurs (*Platypterygius longmani*) consumed this food source (Kear et al. 2003).

Some turtle species have an undisputed keystone role in their environment, exerting "influences on the associated assemblage, often including numerous indirect effects, out of proportion to [their] abundance or biomass" (Paine 1995). Aldabra giant tortoise populations on Aldabra Atoll form what is potentially the largest tortoise concentration on Earth in perhaps the only terrestrial ecosystem dominated by a reptilian herbivore (Stoddart and Serge 1983). Tortoises of average mass (20–30 kg) on Aldabra may eat as much as 79 kg of forage per year (Coe et al. 1979). With an estimated population of 150,466 animals in 33.6 square kilometers (km^2 ; 4478 tortoises per km^2), that amounts to consumption of almost 12 million kg per year. The environmental impact of that many tortoises results in landscape-level changes, including modification of the plant community from coastal, maritime, scrub-tussock vegetation to one of short, turf grassland (Hnatiuk et al. 1976). With an estimated gross assimilation efficiency of 50% (Coe et al. 1979), roughly 6 million kg of vegetation is converted into tortoise biomass each year. Another tortoise species endemic to Madagascar, the radiated tortoise (*Astrochelys radiata*), formerly achieved estimated population densities of up to 5744 per km^2 (Leuteritz et al. 2005) prior to widespread poaching for bush meat and the pet trade (O'Brien et al. 2003), with as yet unknown ecological consequences.

The loss of turtles from an ecosystem can lead to significant environmental consequences. For example, populations of small estuarine diamond-backed terrapins (*Malaclemys terrapin*) are members of a guild of top-down predators that regulate grazing species, such as salt-marsh periwinkle snails (*Littorina irrorata*). Without the effect of these predators, periwinkle snails can convert productive grasslands in salt marshes to barren mudflats in 8 months under experimental conditions (Silliman and Bertness 2002). Other descriptions of the effects that turtles have on ecosystems are described in the section on ecosystem restoration.

Predators (e.g., consumers) exhibit strong direct and indirect effects on ecosystem structure, function, and resilience, often referred to as *top-down effects*. Turtles assume

all the traditional trophic positions of consumers; therefore, the removal or extirpation of turtles could have profound effects on the structure and function of terrestrial, freshwater, and marine communities. For instance, the removal or diminished role of turtles in the wild can be far-reaching and create trophic cascades, altered biomass structure, loss of community function, and invasive species resilience, all of which are critical to maintaining healthy ecosystems. Unfortunately, empirical data reporting these top-down effects caused by turtles are scarce in the scientific literature.

The top-down effects of sea turtles on seagrass meadows and coral reefs are relatively well known. Green turtles (*Chelonia mydas*) can alter the physical structure and flowering of seagrass meadows by heavy, sustained grazing (Lal et al. 2010), which decreases self-shading and reduces detritus, nitrogen, and sulfides in the sediments and associated microbial communities (Thayer et al. 1982). In addition, green turtles directly alter the vegetation community composition of the seagrass meadows, which indirectly diminishes prey refugia and recruitment (see Lal et al. 2010). Furthermore, hawksbill turtles (*Eretmochelys imbricate*) often provide top-down indirect effects on coral reef ecosystems. These sea turtles directly consume sponges, which are competitively superior to coral, thus reducing competition for space within the coral reef and increasing coral species richness and health. The roles of sea turtles are now greatly diminished because of years of global overexploitation (Jackson et al. 2001), and we are just now beginning to understand the consequences.

As freshwater predators, aquatic and semiaquatic freshwater turtles may have strong direct effects on prey abundance but also indirect effects that shape communities as well. For example, the presence of a common freshwater species, the slider turtle, significantly altered environmental characteristics (e.g., pH, conductivity, and sedimentation accumulation) and increased nutrient input into an experimental freshwater pond system (Lindsay et al. 2013). In addition, the increased nutrient load associated with turtle presence in the experimental ponds drove a significant increase in invertebrate abundance and density in the system. Similarly, in ephemeral freshwater ponds, increased nutrient influx provided by the common snapping turtle (*Chelydra serpentina*) positively affected the lowest trophic position of the food web, phytoplankton (Wilbur 1997).

In aquatic ecosystems, in which turtles occupy the highest trophic position, as apex predators, their long-term or temporary presence can have strong effects on ecosystem dynamics. For example, in freshwater mesocosms, common snapping turtles directly altered amphibian community compositions and body condition of prey (Garig 2017). Altered dynamics of lower trophic levels in these mesocosms exposed to turtles were documented over several weeks, even though the turtles were introduced and removed over a 4-day period, demonstrating short- and potentially long-term (e.g., legacy) top-down effects of an apex turtle predator on community structure and function. Consequently, the

extirpation or a diminished role of turtles in a freshwater community could have cascading effects at multiple trophic levels and environmental conditions, shifting short- and long-term ecosystem processes.

Seed dispersal and germination enhancement

The majority of temperate and tropical woody plants depend on vertebrates for seed dispersal (Howe and Smallwood 1982). Therefore, this ecosystem service is vital for maintenance of terrestrial ecosystems globally (Wang and Smith 2002). Turtles have long been overlooked as important seed dispersers; however, several species have been identified as important agents for seed dispersal and germination enhancement of plants. For example, Galápagos tortoises (*Chelonoidis* spp.) regularly move large quantities of seeds over long distances, averaging 464 seeds of 2.8 plant species per defecation event (Blake et al. 2012). Braun and Brooks (1987) fed wild fruits to captive eastern box turtles (*Terrapene carolina*) to determine germination potential. Eleven of 15 species germinated, and 5 had higher germination potential following digestion. In fact, the eastern box turtle is the only known seed dispersal agent for the mayapple (*Podophyllum peltatum*). Mayapple seeds eaten by this turtle species germinate faster and have a higher probability of success than noningested seeds (Rust and Roth 1981). Fecal samples of the leopard tortoise (*Geochelone pardalis*) in South Africa contained 75 plant species belonging to 26 families. Viable seeds were observed for seven plant families on the basis of germination trials, but data were not presented to indicate enhanced germination following digestion (Milton 1992). The majority of seedlings that germinated were grasses. Similar dispersal and germination enhancement capabilities were documented for the Greek tortoise (*Testudo graeca*; Cobo and Andreu 1988), with 6.5%–34.2% of ingested seeds passing through the digestive system in the feces.

Rose and Judd (1982) conducted one of the most thorough analyses of germination enhancement in a tortoise. They demonstrated that seeds of the cactus *Opuntia lindheimeri* passed through the alimentary tract of Texas tortoises (*Gopherus berlandieri*) had a significantly higher germination rate (17%) than those that did not (1.7%). In contrast, seeds maintained in an anoxic environment of nitrogen for 24 hours showed no increase in germination (1%) over controls. Seeds placed in a solution of hydrochloric acid with a pH of 3.5 for 12 hours had significantly lower germination rates (5%) than seeds passed through a tortoise, but the rate was not significantly different from that of the controls. Finally, 80% of the seeds scarified by the researchers germinated, so some form of animal-induced damage or digestion of the seed is beneficial. The authors suggested that seeds passed in fecal pellets have a selective advantage in that they germinate quickly in the presence of water and have a nitrogen source for early development.

Another interesting example of seed dispersal—and, presumably, germination enhancement—involves the declining tambalacoque trees (*Sideroxylon sessiliflorum* and



Figure 3. Gopher tortoise (*Gopherus polyphemus*) burrows provide shelter for over 350 vertebrates and invertebrates (Johnson et al. 2017), many of which cannot dig burrows on their own. Included are burrowing owls (*Athene cunicularia*), various species of lizards, gopher frogs (*Lithobates capito*), red foxes (*Vulpes vulpes*), bobcats (*Lynx rufus*), rodents, rabbits, and snakes, including other declining species, such as eastern indigo snakes (*Drymarchon couperi*) and diamondback rattlesnakes (*Crotalus adamanteus*).

S. grandiflorum) of Mauritius and the extinct giant tortoises (*Cylindraspis* spp.) that lived on the island. The extinction of the dodo bird (*Raphus cucullatus*) has been suggested as an explanation for the declining trees, because dodos may have abraded the thick endocarp of the seed and facilitated germination. However, Iverson (1987) provided sufficient evidence to suggest that the extinct tortoises ate the seeds and facilitated germination. Similar scenarios may have existed between extinct tortoises and an extant baobab tree (*Adansonia rubrostipa*) in Madagascar (Andriantsaralaza et al. 2013). Galápagos tortoises enhance germination of Galápagos tomatoes (*Lycopersicon esculentum*; Rick and Bowman 1961), and the Aldabra giant tortoise may have been responsible for the introduction of plant species to Aldabra from as far away as Madagascar when their ancestors rafted to the distant islands. Twenty-eight species of grasses, herbs, and woody plants have been documented to germinate from the feces of Aldabra giant tortoises (Hnatiuk 1978).

The seed dispersal and germination enhancement abilities of turtles and other members of the seed-eating guild can have a strong influence in the composition of plant communities they occupy. The habit of the black wood turtle (*Rhinoclemmys funerea*) to emerge and defecate on river banks may contribute to the establishment of certain riparian plant species, and the foraging activity of the furrowed wood turtle (*Rhinoclemmys annulata*) may contribute to the distinctive flora of treefall areas in the forest (Moll and Jansen 1995). Similar roles can be envisioned for other species of turtles such as alligator snapping turtles (*Macrochelys temminckii*) that feed on the fruits

of riverine plant species including acorns (Elbers and Moll 2011).

Bioturbation: The role of turtles in soil dynamics

Digging and burrowing animals, including some tortoises, can have an enormous impact on soil processes including its formation, function, and maintenance. Animals living in the soil body and intimately associated with it are considered part of the soil, and animals living above the soil make contributions to it (Hole 1981). In a major review of the effects of animals on soil, Hole (1981) identified 12 effects: mounding, mixing, forming voids, back-filling voids, forming and destroying peds (soil particles), regulating soil erosion, regulating movement of air and water, regulating plant litter, regulating animal litter, regulating nutrient cycling, regulating biota, and producing special constituents. Turtles have a role in many of these processes.

Some turtles are prodigious burrowers, including Agassiz's desert tortoise and the gopher tortoise. Their impressive burrows, sometimes over 10 meters (m) in length for gopher tortoises, qualify them for the title of *ecosystem engineers* because of the impact of burrows on soil layers, water and gas diffusion, and surrounding vegetation. The excavated mounds in front of burrows contribute to environmental heterogeneity and increased plant species diversity (Kaczor and Hartnett 1990). In addition, their burrows are used by over 350 other species (figure 3) as symbiotic occupants (Johnson et al. 2017) that sometimes make secondary and tertiary contributions to burrow architecture by constructing side burrows (Kinlaw and Grasmueck 2012). Given the high densities these tortoises previously achieved and their habit of using more than one burrow per year, they exerted a strong influence on soils before their populations declined (Ernst and Lovich 2009). Catano and Stout (2015) concluded that gopher tortoises were keystone species and ecosystem engineers by virtue of their burrowing habit. They predicted that continued population declines of tortoises will have “large, negative impacts on vertebrate diversity” (p. 1957) in longleaf pine ecosystems and that gopher tortoise populations were critical for conservation of other species that rely on tortoise burrows as well as ensuring ecosystem function.

An example of the degree of soil disturbance that turtles are capable of achieving is shown in nesting green turtles and loggerhead sea turtles on Heron Island, Australia. These species exert a profound effect on the fringing vegetation of the island. Thousands of turtles nest during the period from October to March, affecting a swath of coastal vegetation

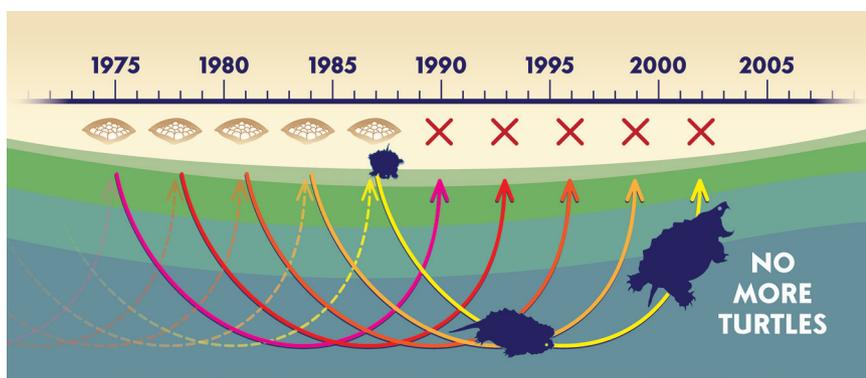


Figure 4. Representation of the perception of persistence in turtles, based on hypothetical results of killing 100% of female alligator snapping turtles in a population before they can nest. This scenario can also happen because of total nest predation, or destruction of all nesting beaches in an area. If it takes 15 years for females to reach maturity, and no more nests are produced after 1987, by about the year 2002, there are no more females left to nest, despite the appearance of returning adult turtles every year from 1987 to 2002. Modified from Mortimer (1995) with permission.

averaging 14.8 m wide by uprooting plants, burying others with sand, flattening small shrubs and breaking branches off of larger shrubs. A single turtle can affect an area of over 2 m in diameter (Rogers 1989).

Loggerhead sea turtles in Moreton Bay, Australia, use an unusual foraging strategy that causes considerable disturbance to the seafloor (Preen 1996). To gain access to buried food sources, loggerhead sea turtles dig pits up to 1.5 m in width and 0.3–0.45 m in depth. Turtles advance through the sediment, eroding the quarry face of the excavation with their front flippers and feeding on invertebrates that are dislocated from their hiding places. At favored feeding sites, approximately 5% of the surface sediments are mined to a depth of 40 cm. Including the lateral sedimentation of spoils from the excavation activity, 8.4% of the areas were affected by turtles. Preen (1996) concluded that foraging disturbance by loggerhead sea turtles had a substantial impact on the biomass, species composition, and dynamics of some seagrass beds and associated fauna. A similar conclusion was reported by Lazar and colleagues (2011) for loggerhead sea turtles in the neritic zone of the northern Adriatic Sea. They stated that foraging behavior by loggerhead sea turtles actively reworks marine sediments and increases the rate of mollusk shell disintegration. They conservatively estimated that loggerhead sea turtles there bioturbate about 33 metric tons of mollusk shells per year. In addition, infaunal mining of invertebrate prey by loggerhead sea turtles may be important in nutrient transfer in marine ecosystems.

Turtles can even be used to restore degraded ecosystems

One of the benefits of understanding the functional role of organisms is the potential ability to harness ecological services they provide. For example, failure to recognize the

ecological role of turtles in maintaining habitat heterogeneity has resulted in losses of certain habitat features, such as small wetlands, and the extinction or decline of some plant species (Iverson 1987, Griffiths et al. 2011, Froyd et al. 2014). Consider the value of turtles in cleaning rivers polluted with corpses in India or scavenging for carrion, as was discussed previously. The ability of some turtles to thrive in polluted waterways (Moll 1980) makes them a tangible benefit.

Tortoises are being used to restore ecosystems long deprived of the effects of their formerly large populations in the Galápagos. Hundreds of thousands of tortoises were removed from the islands over the centuries (MacFarland et al. 1974), severely depleting some stocks and causing the extinction of other species (e.g., Edwards et al. 2013).

By virtue of the tortoises' size, numbers, and role in seed dispersal and germination, vegetation changes occurred after their numbers declined. Since then, tortoise reintroduction efforts are having a positive effect on a rare keystone species of tree-like cactus (*Opuntia megasperma* var. *megasperma*; Gibbs et al. 2008). The selection of tortoise species is important for the success of reintroduction for ecological restoration of some plant species, because not all tortoise species have the same effect or food preferences (Hunter et al. 2013). Tortoise densities do not have to be particularly high to reverse woody plant encroachment in the Galápagos and restore plant communities to more natural conditions (Hunter and Gibbs 2014). Similar efforts are underway with giant tortoises in the Indian Ocean (Griffiths et al. 2011). Even small tortoise species are potential substitutes for the seed dispersal services formerly provided by extinct larger mammal species in defaunated continental forests (Sobral-Souza et al. 2017).

Conclusions

The declines and extinctions of turtle populations globally mean that their ecological roles are now greatly diminished from times when turtles were more abundant. The impacts of their lessened roles are poorly appreciated and inadequately understood. More definitive studies are needed to demonstrate the direct and indirect consequences of removing turtles from ecosystems.

Two possible reasons exist for why society tends to overlook the decline of turtles. The first is what we call the *perception of persistence*. Turtles of many species have the ability to live a long time, occasionally exceeding 100 years (Gibbons 1987, Ernst and Lovich 2009). Some species also take a long time to reach sexual maturity and have long reproductive lifespans (Congdon et al. 1994). Mortimer

(1995) presented an elegant example of a hypothetical sea turtle population that required 25 years to reach sexual maturity. In Mortimer's scenario, humans began killing every female sea turtle that returned to nest after a certain date. This is a plausible scenario, because of all reptiles used by humans as a food source, turtles are the most heavily exploited (Klemens and Thorbjarnarson 1995), and turtle extinctions from overharvest are well-documented (Turtle Extinctions Working Group 2015). Because of the success of previous nests prior to overexploitation and the long time it took those turtles to reach sexual maturity, a casual observer on the beach would see turtles return to be slaughtered for over two decades before there were no more sea turtles left to return (see figure 4 for an example of another heavily exploited turtle species). The persistence of adult turtles in a population for years does not necessarily mean that recruitment is taking place that will replace those adults when they die over the course of many years. Any time the rate of deaths exceeds births, a population will decline. Populations without recruitment are demographically decadent, to borrow a term long used by foresters to describe old trees.

The second reason turtle declines are overlooked relates to shifting baselines involving “changing human perceptions of biological systems due to loss of experience about past conditions” (Papworth et al. 2009, 93). People born into a world without large numbers of turtles performing important ecosystem functions accept that as the new norm (e.g., de Miranda 2017). A recent example involves a now cosmopolitan species of invasive turtle known as the red-eared slider (*Trachemys scripta elegans*). The species is introduced and thriving all over the temperate world from their humble origins in southern North America. Sliders often do very well in their new environments, sometimes to the detriment of other native turtles (e.g., Taniguchi et al. 2017). As a result of their ubiquity and shifting baselines in Japan, a cultural transition in public awareness may have occurred in the perception of what constitutes a *native* turtle (Lovich and Yamamoto 2016). People seeing large numbers of exotic slider turtles in urban or agricultural ponds might be duped into thinking that turtles are doing well, without recognizing that sliders are not native to the area and, in many situations, replace the indigenous turtle species, thus reducing the diversity of native species.

As the only reptiles that are universally liked by people, it would be a sad world indeed to lose more of these iconic and remarkable survivors from the mists of deep evolutionary time. They survived the Cretaceous–Paleogene boundary cataclysm that wiped out the dinosaurs. Will they survive us in the Anthropocene?

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