

Range map of the Galapagos shark



The largest number and highest diversity of fish are found in places with sharks. Photo credit: iStock/Getty Images Plus

Coral reefs are a critical marine habitat. Even though they cover less than 1% of the ocean, they support an estimated 25% of all marine species. However, humans have negatively impacted reefs for at least 500 years — in part through the overfishing of large species at the top of the food chain, such as sharks and other predatory fish. One example, the Galapagos shark, has been hunted for its meat and fins.

Scientists are investigating how the ongoing loss of top predators affects reef ecosystems. Although reefs unaffected by humans are rare, which makes this research challenging, scientists have been able to

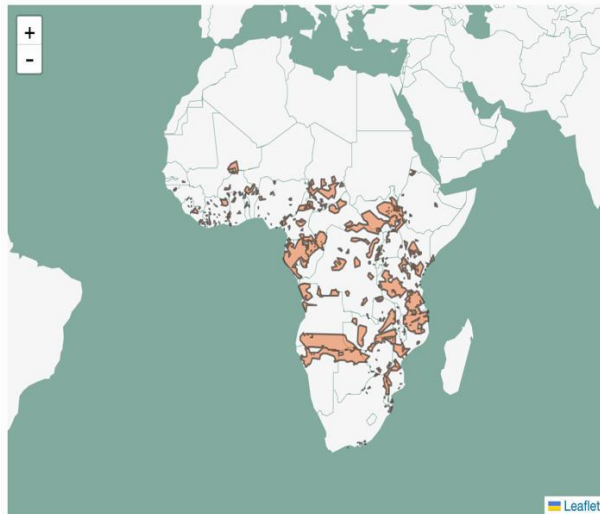
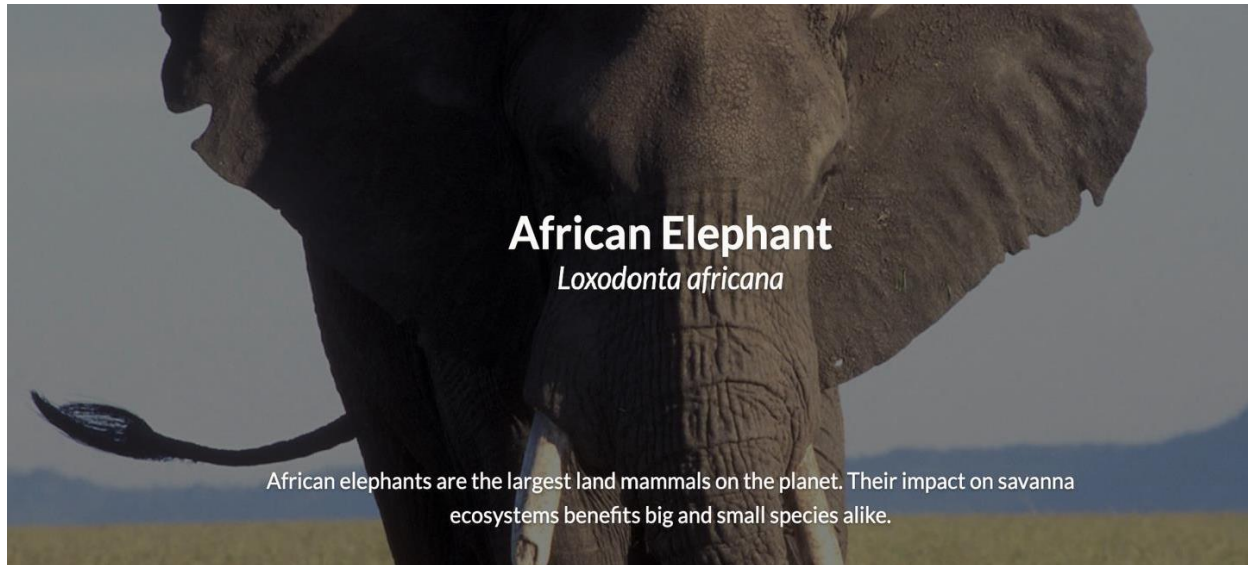
study reefs with and without sharks near Hawaii. Top predators, including the Galapagos shark, are generally absent from reefs near the main Hawaiian Islands. However, these predators are still present in reefs near the northwestern Hawaiian Islands: a large, remote, lightly fished area that is otherwise similar to the main islands.

The study found that the absence of top predators changes the overall community of reef fish. Reefs with top predators tended to have more diversity, larger fish, and fish occupying a greater variety of trophic levels. In contrast, reefs without top predators had less diversity overall and were dominated by small herbivorous fish. These herbivorous fish eat the algae growing on the reef, which may impact other organisms that use the algae.

Although sharks and other top predators are clearly important for maintaining the balance of an ecosystem, one can argue that humans exert the ultimate control. Examples like these have been used to debate whether humans are the ultimate keystone species, as impacts of human activity are widespread across almost all ecosystems.

<https://media.hhmi.org/biointeractive/click/keystone/shark.html>





Range map of the African elephant



Elephants on the savanna Photo credit: iStock/Getty Images Plus

Elephants are famous symbols of the African savanna, but they are less known for their role as **ecosystem engineers**: organisms that create, change, or maintain habitats. Elephants transform their habitats in a variety of ways: by knocking down trees, pulling up grass, plowing trails through dense plants, and digging water holes that other animals can use. Scientists have observed these impacts for decades. More recently, they've started studying the broader effects of elephants on species diversity.



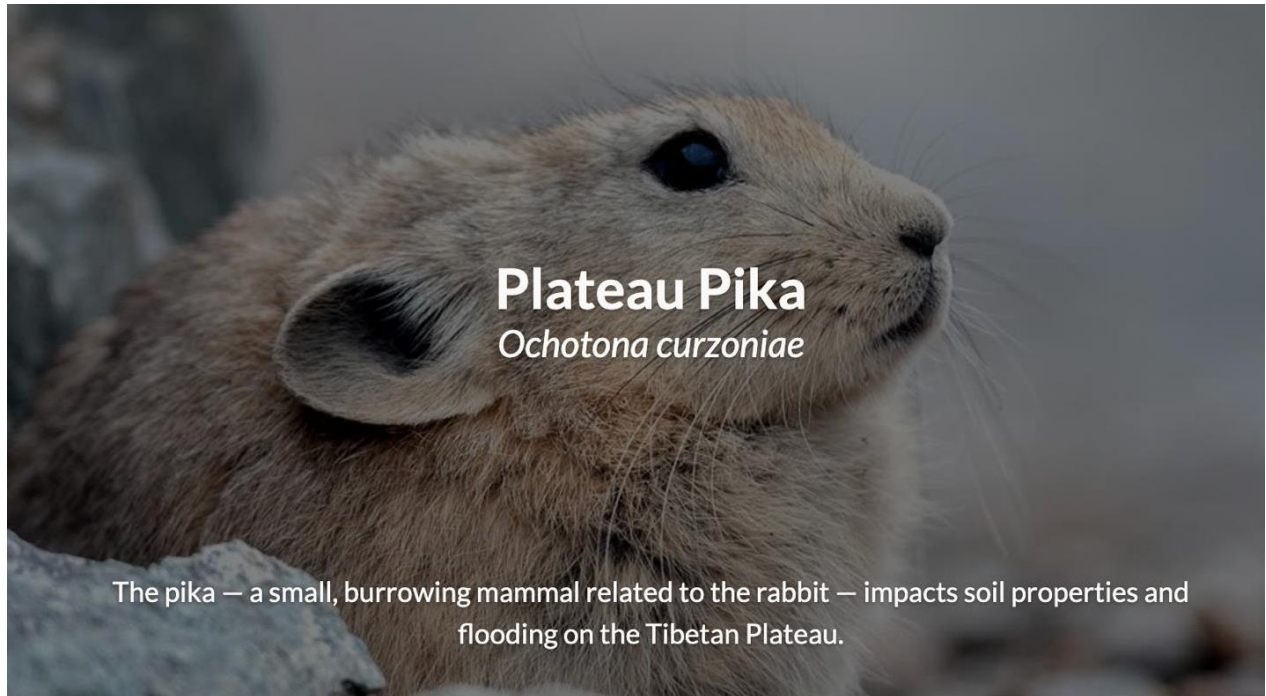
Elephants often break branches and knock down trees, creating more habitat for smaller animals. Photo credit: iStock/Getty Images Plus



An elephant next to a large branch Photo credit: iStock/Getty Images Plus

Scientists compared similar areas where elephants were either present or absent. Areas where elephants were present had a greater diversity of small reptiles and amphibians. One possible explanation is that trees damaged by elephants provide habitats for communities of smaller animals.

<https://media.hhmi.org/biointeractive/click/keystone/elephant.html>



The Tibetan Plateau has one of the highest grassland ecosystems in the world. Over recent decades, its grasslands have declined — due in part to overgrazing (that is, livestock eating too much of the grass). This has also led to an increase in the number of pikas, who thrive in the less grassy areas. Some people thought that the pikas were causing the change in the grasslands. In 1958, the Chinese government began programs to exterminate pikas.

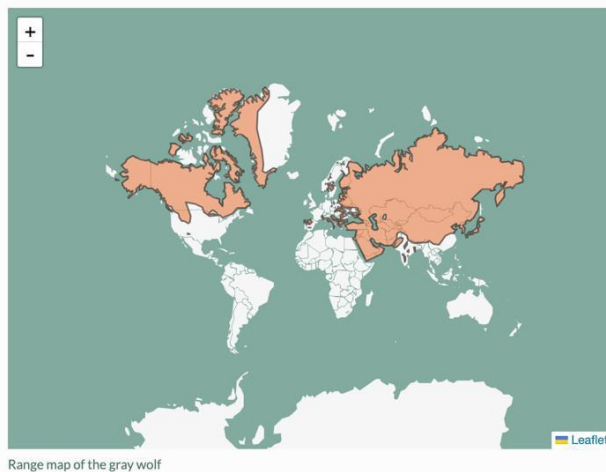


Pikas live in burrows that they dig and maintain over time. *Photo credit: iStock/Getty Images Plus*

More recently, scientists compared areas with and without pikas to better understand their effects. Areas with pikas have more burrows, large systems of underground tunnels that the pikas dig for shelter. The scientists discovered that pikas' burrows help the soil hold more water. This can reduce flooding during the wet season and makes it less likely that rivers will dry up at other times of the year.

So, contrary to what people had initially thought, pikas appear to benefit the ecosystem by improving the quality of the soil. Exterminating pikas may thus have unwanted consequences — not only for the Tibetan grasslands but also for human society. About 20% of the world's human population lives downstream of the Tibetan Plateau. They may be at risk of seasonal flooding and water shortages in the absence of pikas and their burrows.

<https://media.hhmi.org/biointeractive/click/keystone/pika.html>



Gray wolves used to roam across wide portions of North America, all the way from Alaska to Mexico. As humans developed these areas, wolves and many other top predators were killed or pushed out. They were even eliminated from some protected areas, such as Yellowstone National Park.

After wolves disappeared from Yellowstone, the size of the park's elk population exploded. The elk ate many plants, especially young seedlings and willows, growing along the rivers. Normally, the roots of these plants help hold the soil in place. So the dramatic decrease in these plants led to erosion along the riverbanks, which destroyed

habitats for animals like beavers and songbirds.

In 1995, the federal government of the United States began a program to reintroduce wolves to Yellowstone. In the decades after wolves returned to the park, the elk population declined, the willow population recovered, and the health of the park's ecosystem stabilized.



Elk grazing near a river. In the absence of wolves, the elk often ate too many plants. Photo credit: iStock/Getty Images Plus



A river habitat with many plants. Habitats like these recovered after wolves returned and began controlling the elk population. Photo credit: iStock/Getty Images Plus

In 1995, the federal government began a program to reintroduce wolves to Yellowstone. In the decades since, the elk population declined, willows rebounded, and the health of the whole ecosystem stabilized.

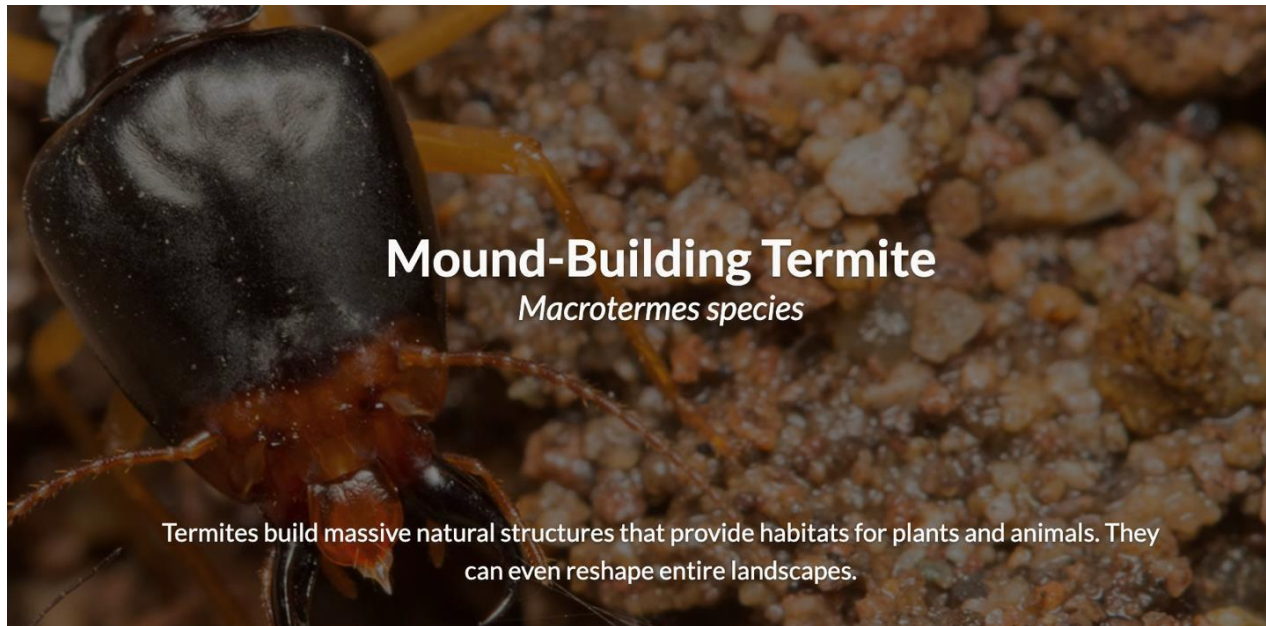
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Around the world, there are 65 species of flying foxes — also known as fruit bats. Some of these species are among the largest-known groups of bats alive today, and about half are threatened by invasive species, hunting, and habitat loss.

Flying foxes are a group of fruit bats with 65 species around the world. Some of these species are among the largest bats alive today. About half are threatened by hunting, habitat loss, and invasive species. One example is the Samoan flying fox, which lives on the South Pacific islands of Fiji, Samoa, and American Samoa.

<https://media.hhmi.org/biointeractive/click/keystone/flying-fox.html>



Termites are considered pests in some parts of the world. But these common insects play crucial roles in savannas ranging from Australia to Africa. For example, termites feed on dead plant material, which helps clean up habitats and cycle nutrients through ecosystems.

Mound-building termites are also **ecosystem engineers**: organisms that create, change, or maintain habitats. These termite species build large structures called termite mounds, which house huge colonies of termites. Some mounds are as high as 5 meters tall and extend deep underground.



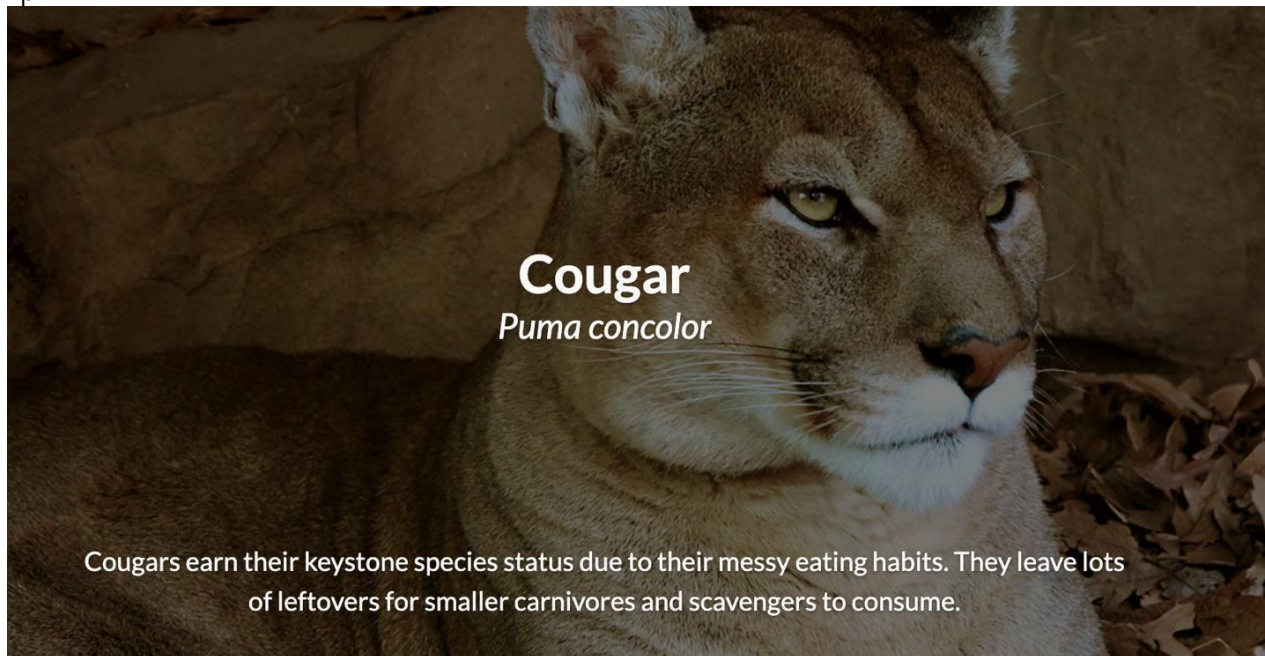
Termite mounds in an Australian savanna. Mounds like these improve soil moisture and are hotspots for nutrient cycling. *Photo credit: iStock/Getty Images Plus*

Termite mounds are important for the health of savanna ecosystems. They improve soil properties, increase the availability of nutrients, and make it easier for water to move through the ground — all of which helps nearby plants grow.

In addition, local animals use the mounds for a variety of purposes. Some use the mounds as lookouts, to either find prey or avoid predators. Others use the mounds as a source of food, eating the plants that grow on them and the termites themselves. Dozens of species also use abandoned mounds as new homes.

<https://media.hhmi.org/biointeractive/click/keystone/termite.html>

Fp



The cougar, also known as the puma or mountain lion, is a large predator that usually hunts alone. Its range spans most of the Americas, from Canada down to Chile.

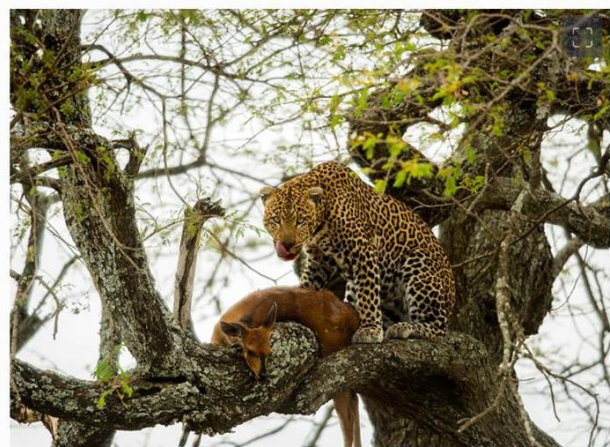
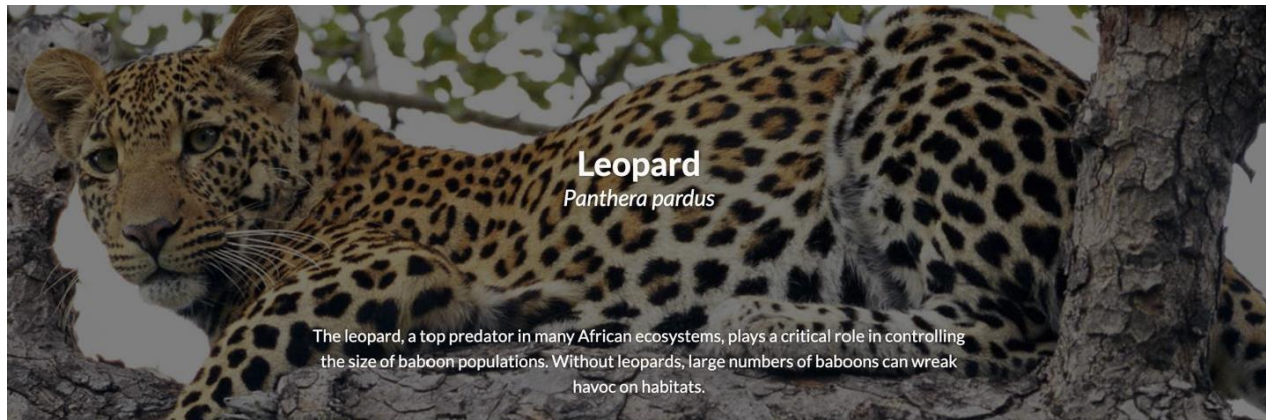
In the South American region of Patagonia, scientists have been using GPS collars to track cougars and observe their feeding behavior. This research has led to a new understanding of how cougars help cycle nutrients in the Patagonian ecosystem.



Andean condors are scavengers that depend on carrion. In one study, they were observed at 43% of puma kills.

The scientists discovered that the Patagonian cougars are “messy eaters.” They leave behind a large amount of meat compared to other top predators. These leftovers are an important food source for scavengers, such as the Andean condor. These cougars also frequently abandon fresh kills, possibly to avoid being bothered by scavengers or seen by human hunters. Their abandoned food can feed smaller carnivores.

<https://media.hhmi.org/biointeractive/click/keystone/cougar.html>



Around the world, populations of top predators have been declining due to habitat loss, hunting, and poaching. Leopards — which are native to habitats in Africa and Asia that include deserts, savannas, mountains, and rainforests — are one major predator threatened with extinction.

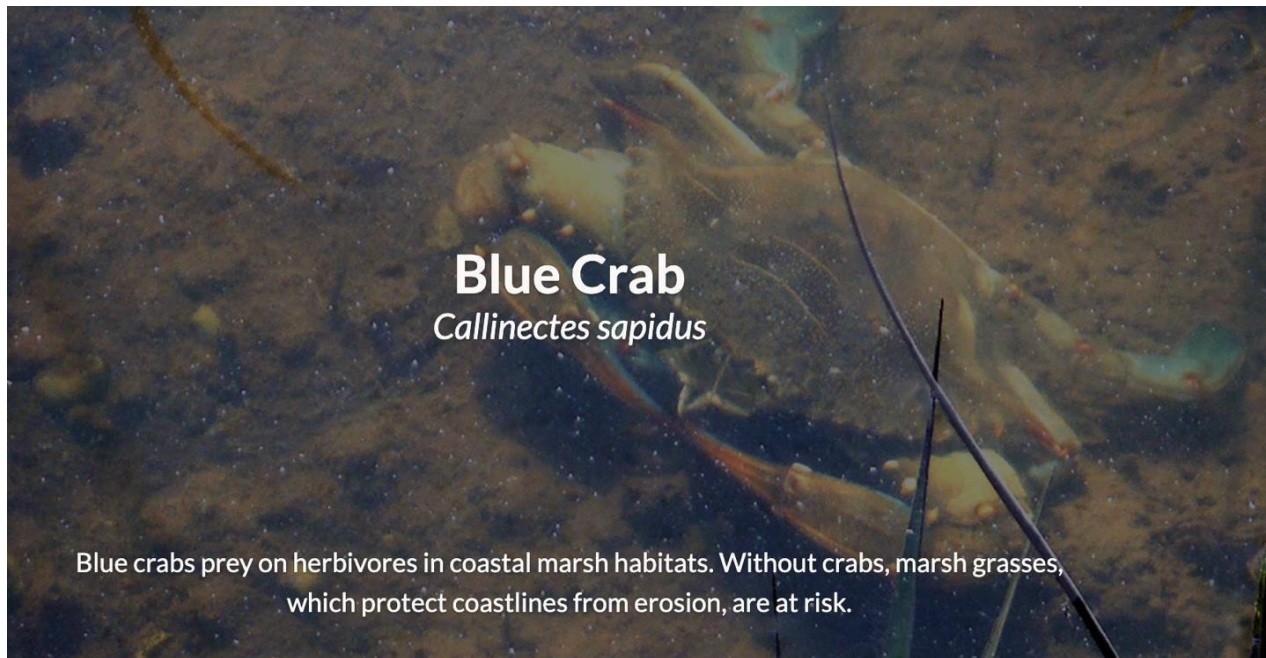
As leopards have declined, populations of the species they prey on, such as baboons, have grown rapidly. From 1968 to 2004, for example, leopards disappeared from several national parks in the West African country of Ghana. Scientists recorded a 365% increase in the local baboon populations over this time.



Baboon population sizes exploded as leopards and other big cats declined. *Photo credit: iStock/Getty Images Plus*

With fewer leopards, baboons not only increase in number but also behave differently. They spend more time on the ground than in the safety of the trees, eating more of the eggs of ground-nesting birds and raiding human crops. Baboons also eat a much larger variety of things than their predators do, including insects, birds, eggs, reptiles, mammals, fish, and fruits. When baboon populations grow, they eat more of all of these things, which has large effects on the ecosystem.

<https://media.hhmi.org/biointeractive/click/keystone/leopard.html>



Range map of the blue crab



Blue crabs live in salt marshes like this one. The salt marsh is a coastal ecosystem found all over the world.
Photo credit: iStock/Getty Images Plus

Scientists wanted to know what determines the abundance of plants in a Salt marshes are common ecosystems on the coasts in temperate climates. They offer a number of **ecosystem services** (benefits provided to humans by ecosystems), including pollution filtration, protection from erosion, and nurseries for many fisheries. Because of the importance of marshes, scientists and conservationists study the stability and resilience of these ecosystems.

salt marsh. The abundance of plants in an ecosystem can be driven from the **bottom up** (by resources such as water, light, and nutrients) or from the **top down** (by animals such as herbivores and their predators). To test

these two possibilities, the scientists set up an experiment in a Georgia salt marsh. Their experiment focused on marsh grass, the main plant in the marsh, and the periwinkle snail, the main herbivore that eats marsh grasses.

The scientists built cages over some areas of the marsh to keep periwinkle snails from getting in and out. Over time, they compared areas of the marsh with and without snails. In areas where snails were present, the marsh grasses were greatly reduced. In areas where snails were absent, the grasses grew more and had better survival. Based on these results, the scientists concluded that the abundance of plants in a salt marsh is determined from the top down.

So what keeps the snails from eating all the marsh grasses normally? To answer this question, the scientists investigated the role of blue crabs, one of the snails' main predators. This time, they set up cages to keep crabs in or out of certain areas. In areas where crabs were absent, snails ate all the grass, and the marsh became a bare, muddy area called a **mudflat**. In areas where crabs were present, the grasses survived, and the marsh stayed healthy.

The scientists concluded that blue crabs keep the snail population from becoming too large. When crabs are absent (for example, from overfishing), the snails may destroy the marsh grasses and turn the marsh into a mudflat. Mudflats provide fewer ecosystem services compared to marshes and put coastlines at risk of erosion.



Marshes are vast habitats that are home to many species. Photo credit: iStock/Getty Images Plus

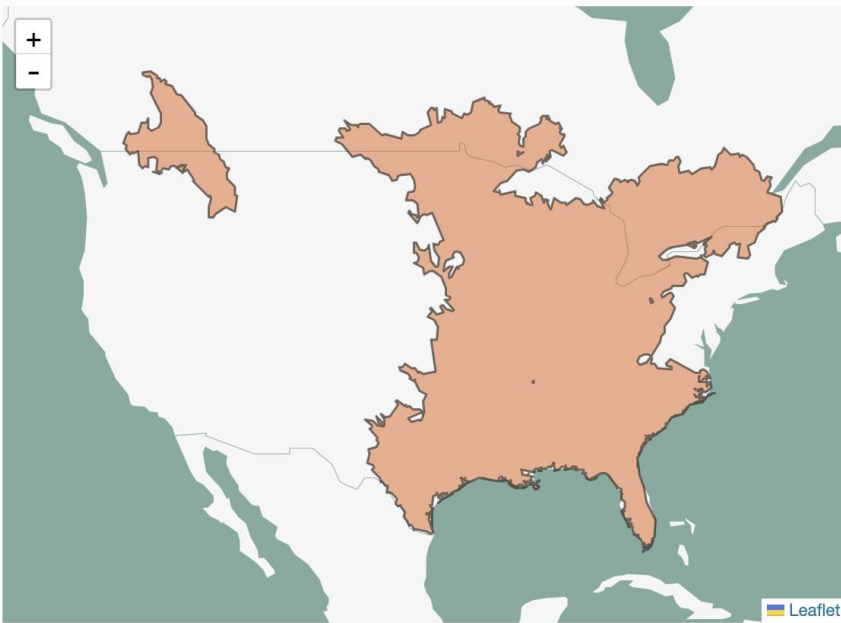


The population density of snails can be in the thousands per square meter of marsh. Photo credit: iStock/Getty Images Plus

Largemouth Bass

Micropterus salmoides

Largemouth bass are top predators in freshwater lakes and rivers. The effects of their presence (or absence) can cascade throughout the ecosystem.



Range map of largemouth bass

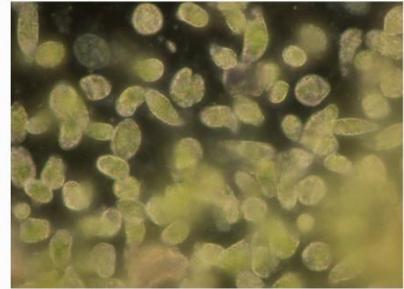
The largemouth bass is a top predator in the lakes of the midwestern United States. These bass often eat smaller fish, such as minnows. Minnows eat zooplankton, which eat phytoplankton (microscopic algae).



Freshwater minnows. They eat zooplankton and are eaten by bass.
Photo credit: iStock/Getty Images Plus



Daphnia, a common species of zooplankton. They feed on phytoplankton. Photo credit: iStock/Getty Images Plus



Euglena, a common species of phytoplankton. They are at the base of the food chain in most freshwater ecosystems. Photo credit: iStock/Getty Images Plus

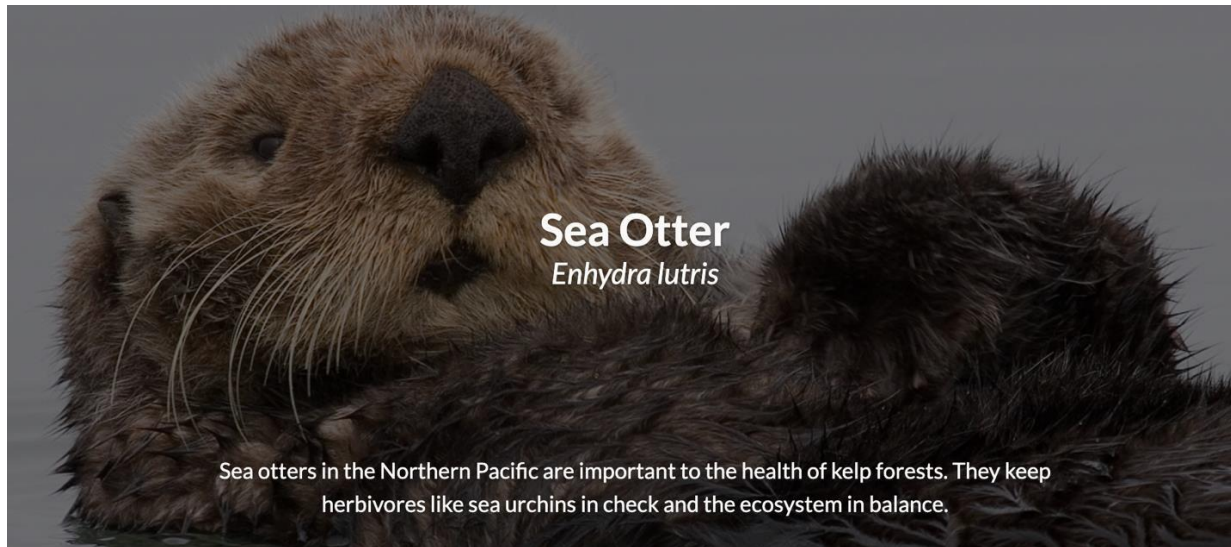
Small lakes, like the ones where these organisms live, are ideal systems for testing the role of a species in an ecosystem. Lakes have clear boundaries, and their food webs are often relatively simple. Scientists can also use neighboring lakes in comparative experiments, which test and compare the effects of different conditions.

To test how the presence or absence of a top predator affects the lake ecosystem, scientists removed largemouth bass from some lakes and not others. The absence of the bass caused minnow populations to increase. More minnows ate more zooplankton. Fewer zooplankton led to a rapid phytoplankton increase called an algal bloom. Algal blooms use up a lot of the oxygen in a lake, which may kill many of the other species. Blooms of certain phytoplankton species can even turn the water toxic.



Two neighboring lakes in Michigan. Scientists removed largemouth bass from the lake on the left, which led to an algal bloom. Photo credit: Stephen Carpenter

<https://media.hhmi.org/biointeractive/click/keystone/bass.html>



Range map of the sea otter

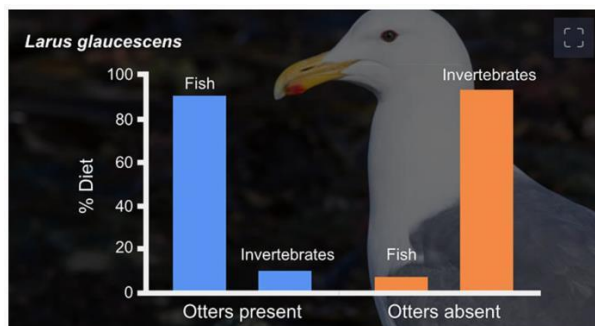
In the past, sea otters numbered in the hundreds of thousands and lived in over a large range: from southern California up the coast to Alaska, across the Kamchatka Peninsula, and down to Japan.

But in the 1700s and 1800s, otters were hunted almost to extinction for their fur. When hunting was finally restricted, otter populations returned to some places but not others. The presence and absence of otters in different locations allowed ecologist Jim Estes to investigate the role of otters in their ecosystems. He focused on **kelp forests** in the

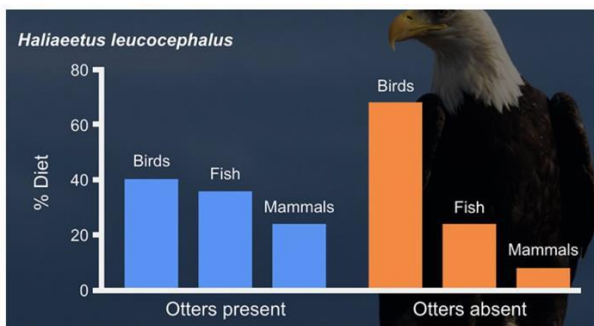
Northern Pacific Ocean, underwater ecosystems that contain many large seaweeds called kelp.

In the kelp forests, otters are the main predator of sea urchins. Estes found that where otters were present, they kept sea urchin numbers in check, preventing the urchins from eating all the kelp. The kelp forests with otters were healthy, providing habitat for thousands of species of fish, seabirds, and invertebrates.

Where otters were absent, the number of sea urchins exploded. The urchins ate much of the kelp, impacting species that rely on the kelp forest ecosystem. The diets of birds that feed on kelp forest species, for example, changed significantly in the absence of otters. Scientists call this type of ripple effect a **trophic cascade**. In this trophic cascade, a change in one species, the sea otter, indirectly affected many other species in the ecosystem.

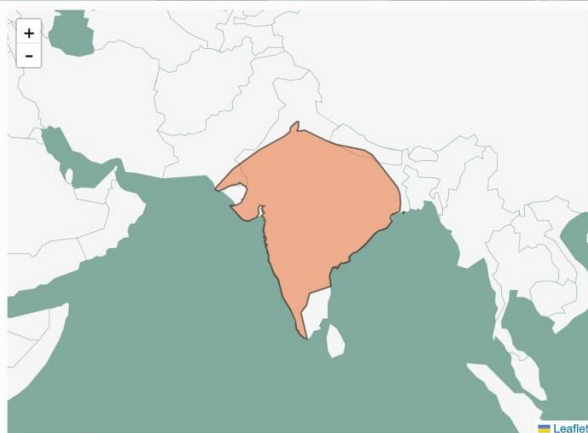


The diets of gulls (*Larus glaucescens*) in the presence and absence of otters



The diets of bald eagles (*Haliaeetus leucocephalus*) in the presence and absence of otters

<https://media.hhmi.org/biointeractive/click/keystone/sea-otter.html>



Range map of the Indian vulture



Although now critically endangered, the Indian vulture was once found across most of the Indian subcontinent. Photo credit: iStock/Getty Images Plus

Although scavengers may seem like unlikely candidates for keystone species, they can play a crucial role by removing rotting meat that would otherwise spread disease. The case of the Indian vulture shows what can happen when certain scavengers almost disappear.

In the 1980s, Indian farmers began treating their livestock with an anti-inflammatory, pain-relieving drug similar to ibuprofen. When livestock animals eventually die, their remains are often left to be consumed by scavengers, either in fields or at carcass dumps. The remains of livestock

that had been treated with the drug turned out to be toxic to vultures, and many of the vultures died after eating them.

The decline in vultures revealed their value to environmental health. For example, vultures have strong stomach acids that kill many pathogens. As vultures died out, these pathogens became more common — leading to diseases in humans and other animals, including tuberculosis, anthrax, brucellosis, and foot-and-mouth disease. As the rotting carcasses increased, some of the pathogens also entered the water supply, which worsened the water quality.

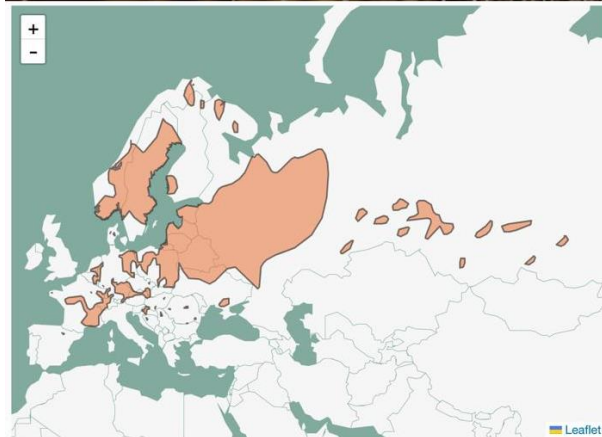
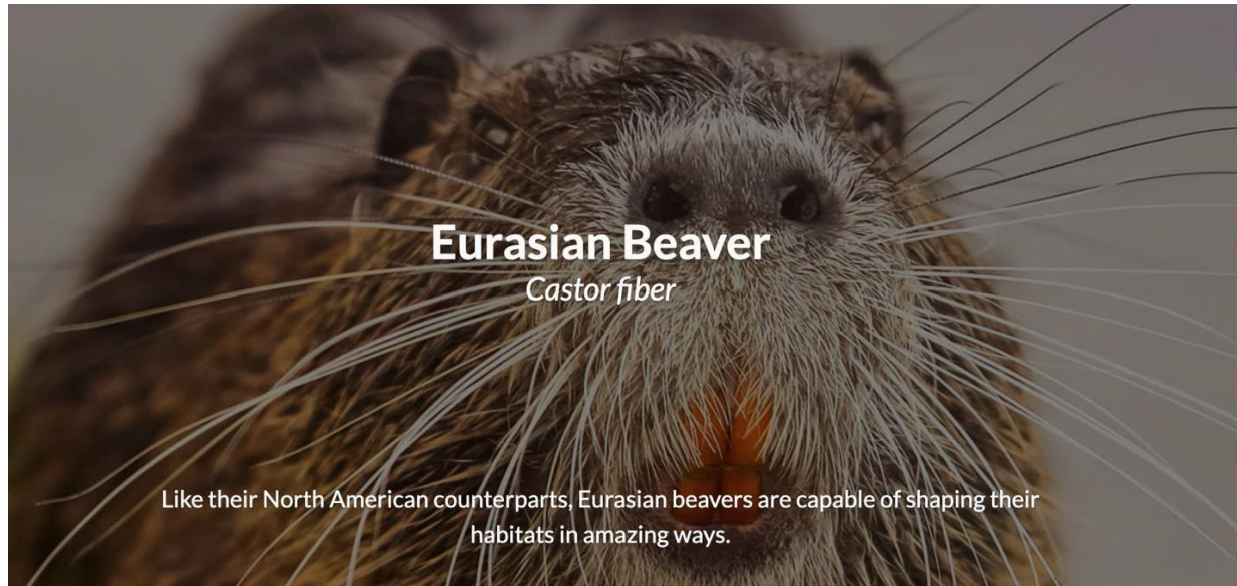
Without as many vultures to compete with, populations of other scavengers, such as crows, rats, and feral dogs, grew rapidly. Some of these scavengers were dangerous to humans. The increase in the number of feral dogs, for example, led to many more dog bites and human deaths from rabies. Scientists estimate that these dogs caused almost 50,000 deaths from 1992 to 2006.



Feral dogs and other scavengers thrived after vultures disappeared. Photo credit: iStock/Getty Images Plus

Scientists eventually realized the impacts of the vultures' disappearance and figured out what was killing them. The livestock drug was banned in India, and the vulture population started to recover.

<https://media.hhmi.org/biointeractive/click/keystone/vulture.html>



Range map of the Eurasian beaver



Beavers use a variety of materials to build their dams, including branches, rocks, and mud. Photo credit: iStock/Getty Images Plus

Beavers are well-known for building dams, large structures in rivers and streams that can cause flooding and create new habitats. In this way, beavers act as **ecosystem engineers**: organisms that create, change, or maintain habitats. The Eurasian beaver has played a key role in shaping marsh habitats across Europe and Asia. In the 1800s, however, farmers began draining the marshes in order to turn them into cattle pastures. The beaver

population nearly died out, and these habitats lost a lot of biodiversity.

In the early 2000s, scientists began reintroducing pairs of beavers to these habitats. As the beavers settled in, they built dams that transformed the terrain. Other plant and animal species took advantage of newly available niches, and biodiversity increased. Today, the habitats where beavers were reintroduced have been restored to a healthier, more natural state.



A meadow, formerly a cattle pasture, in 2003: one year after beavers were reintroduced. It contains relatively few plant species. Photo courtesy of Alan Law



The meadow in 2014: 12 years after the beavers were reintroduced. The number of plant species has increased. Photo courtesy of Alan Law

<https://media.hhmi.org/biointeractive/click/keystone/beaver.html>



Range map of the purple sea star



A healthy population of purple sea stars

In the mid-1900s, ecologists wanted to understand what controls the population sizes of organisms. Ecologist Fred Smith approached this problem by asking a related question: “What keeps the world green?” In other words, what keeps all the plants from being eaten by herbivores?

Smith and his colleagues proposed that predators play a key role in maintaining the numbers of plants in an ecosystem — mainly by limiting the number of herbivores. To test this idea, which became known as the **green world hypothesis**, ecologist Robert Paine looked for an ecosystem in which he could observe the effects of a predator on the rest of the community. He chose tide pools because they have clear physical boundaries and relatively simple food webs.

Paine removed the top predator, the purple sea star, from several North

Pacific tide pools. Then, he observed changes to the remaining plants and animals in the ecosystem.

At the beginning of Paine's experiment, the ecosystem had 16 species. One year later, it was down to eight species. After five years, only one species remained: a type of mussel that was usually preyed on by the purple sea star. The absence of the sea star had allowed the mussel to take over, collapsing the diversity of the ecosystem to a single species.



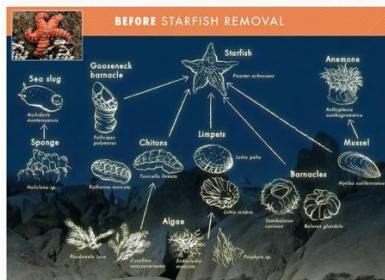
A tide pool at low tide showing diverse organisms, including sea anemones and algae Photo credit: iStock/Getty Images Plus



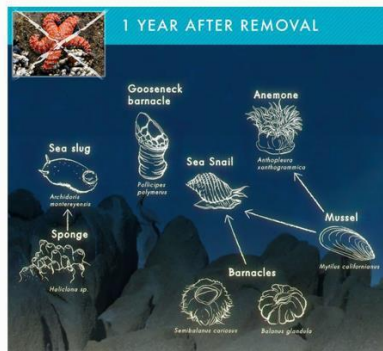
Mussels, one of the species preyed on by purple sea stars Photo credit: iStock/Getty Images Plus



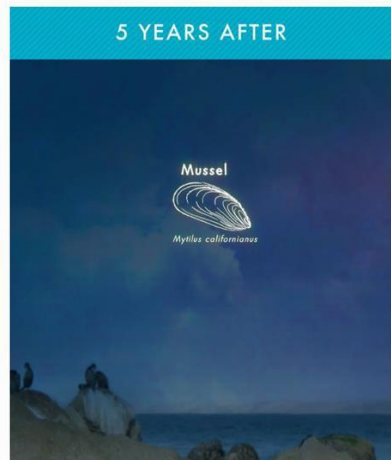
A tide pool without purple sea stars, now dominated by mussels Photo credit: iStock/Getty Images Plus



A food web showing the 16 species in the tide pools at the start of Paine's experiment



A food web of the species one year after removing the purple sea star



The only species remaining five years after removing the purple sea star

Paine tried experiments in which he removed species other than the purple sea star from tide pools. However, the absence of other species did not have such a dramatic impact. In 1969, Paine came up with the concept of a "keystone species" to describe the sea star's unusually large effects. His work inspired decades of research into how the presence or absence of certain species affects ecosystems.

<https://media.hhmi.org/biointeractive/click/keystone/sea-star.html>