Keystone species

A **keystone species** is a species which has a disproportionately large effect on its natural environment relative to its abundance, a concept introduced in 1969 by the zoologist Robert T. Paine. Such species are described as playing a critical role in maintaining the structure of an ecological community, affecting many other organisms in an ecosystem and helping to determine the types and numbers of various other species in the community. Without keystone species, the ecosystem would be dramatically different or cease to exist altogether. Some keystone species, such as the wolf, are also apex predators.

The role that a keystone species plays in its ecosystem is analogous to the role of a keystone in an arch. While the keystone is under the least pressure of any of the stones in an arch, the arch still collapses without it. Similarly, an ecosystem may experience a dramatic shift if a keystone species is removed, even though that species was a small part of the ecosystem by measures of biomass or productivity. It became a popular concept in conservation biology, alongside flagship and umbrella species. Although the concept is valued as a descriptor for particularly strong inter-species interactions, and it has allowed easier communication between ecologists and conservation policy-makers, it has been criticized for oversimplifying complex ecological systems.

History

The concept of the keystone species was introduced in 1969 by the zoologist Robert T. Paine. Paine developed the concept to explain his observations and experiments on the relationships between marine invertebrates of the intertidal zone (between the high and low tide lines), including starfish and mussels. He removed the starfish from an area, and documented the effects on the ecosystem. In his 1966 paper, *Food Web Complexity and Species Diversity*, Paine had described such a system in Makah Bay in Washington. In his 1969 paper, Paine proposed the keystone species concept, using *Pisaster ochraceus*, a species of starfish, and *Mytilus californianus*, a species of mussel, as a primary example. The concept became popular in conservation, and was deployed in a range of contexts and mobilized to engender support for conservation, especially where human activities had damaged ecosystems, such as by removing keystone predators.

Definitions:

A keystone species was defined by Paine as a species that has a disproportionately large effect on its environment relative to its abundance. It has been defined operationally by R. D. Davic in 2003 as "a strongly interacting species whose top-down effect on species diversity and competition is large relative to its biomass dominance within a functional group."[1]

A classic keystone species is a predator that prevents a particular herbivorous species from eliminating dominant plant species. If prey numbers are low, keystone predators can be even less abundant and still be effective. Yet without the predators, the herbivorous prey would explode in numbers, wipe out the dominant plants, and dramatically alter the character of the ecosystem. The exact scenario changes in each example, but the central idea remains that through a chain of

interactions, a non-abundant species has an outsized impact on ecosystem functions. For example, the herbivorous weevil *Euhrychiopsis lecontei* is thought to have keystone effects on aquatic plant diversity by foraging on nuisance Eurasian watermilfoil in North American waters. Similarly, the wasp species *Agelaia vicina* has been labeled a keystone species for its unparalleled nest size, colony size, and high rate of brood production. The diversity of its prey and the quantity necessary to sustain its high rate of growth have a direct impact on other species around it.

The keystone concept is defined by its ecological effects, and these in turn make it important for conservation. In this it overlaps with several other species conservation concepts such as flagship species, indicator species, and umbrella species. For example, the jaguar is a charismatic big cat which meets all of these definitions:

The jaguar is an umbrella species, flagship species, and wilderness quality indicator. It promotes the goals of carnivore recovery, protecting and restoring connectivity through Madrean woodland and riparian areas, and protecting and restoring riparian areas. ... A reserve system that protects jaguars is an umbrella for many other species. ... the jaguar [is] a keystone in subtropical and tropical America ...

— David Maehr et al, 2001

Predators

Sea otters and kelp forests

Sea otters protect kelp forests from damage by sea urchins. When the sea otters of the North American west coast were hunted commercially for their fur, their numbers fell to such low levels – fewer than 1000 in the north Pacific ocean – that they were unable to control the sea urchin population. The urchins in turn grazed the holdfasts of kelp so heavily that the kelp forests largely disappeared, along with all the species that depended on them. Reintroducing the sea otters has enabled the kelp ecosystem to be restored. For example, in Southeast Alaska some 400 sea otters were released, and they have bred to form a population approaching 25,000.

The sea otter is an important predator of sea urchins, making it a keystone species for the kelp forests.

The wolf, Yellowstone's apex predator

Apex predator

Keystone predators may increase the biodiversity of communities by preventing a single species from becoming dominant. They can have a profound influence on the balance of organisms in a particular ecosystem. Introduction or removal of this predator, or changes in its population density, can have drastic cascading effects on the equilibrium of many other populations in the ecosystem. For example, grazers of a grassland may prevent a single dominant species from taking over.

The elimination of the gray wolf from the Greater Yellowstone Ecosystem had profound impacts on the trophic pyramid. Without predation, herbivores began to over-graze many woody browse species, affecting the area's plant populations. In addition, wolves often kept animals from grazing in riparian areas, which protected beavers from having their food sources encroached upon. The removal of wolves had a direct effect on beaver populations, as their habitat became territory for grazing. Increased browsing on willows and conifers along Blacktail Creek due to a lack of predation caused channel incision because the beavers helped slow the water down, allowing soil to stay in place. Furthermore, predation keeps hydrological features such as creeks and streams in normal working order. When wolves were reintroduced, the beaver population and the whole riparian ecosystem recovered dramatically within a few years.[16]

Sea stars and other non-apex predators

As described by Paine in 1966, some sea stars (e.g., *Pisaster ochraceus*) may prey on sea urchins, mussels, and other shellfish that have no other natural predators. If the sea star is removed from the ecosystem, the mussel population explodes uncontrollably, driving out most other species.

These creatures need not be apex predators. Sea stars are prey for sharks, rays, and sea anemones. Sea otters are prey for orca.

The jaguar, whose numbers in Central and South America have been classified as near threatened, acts as a keystone predator by its widely varied diet, helping to balance the mammalian jungle ecosystem with its consumption of 87 different species of prey. The lion is another keystone

Mutualists

Keystone mutualists are organisms that participate in mutually beneficial interaction and the loss of which would have a profound impact upon the ecosystem as a whole. For example, in the Avon Wheatbelt region of Western Australia, there is a period of each year when *Banksia prionotes* (acorn banksia) is the sole source of nectar for honeyeaters, which play an important role in pollination of numerous plant species. Therefore, the loss of this one species of tree would probably cause the honeyeater population to collapse, with profound implications for the entire ecosystem. Another example is frugivores such as the cassowary, which spreads the seeds of many different trees, and some will not grow unless they have been through a cassowary.

Engineers

A term used alongside keystone is ecosystem engineer. In North America, the prairie dog is an ecosystem engineer. Prairie dog burrows provide the nesting areas for mountain plovers and burrowing owls. Prairie dog tunnel systems also help channel rainwater into the water table to prevent runoff and erosion, and can also serve to change the composition of the soil in a region by increasing aeration and reversing soil compaction that can be a result of cattle grazing. Prairie dogs also trim the vegetation around their colonies, perhaps to remove any cover

for predators. Grazing species such as plains bison, pronghorn, and mule deer have shown a proclivity for grazing on the same land used by prairie dogs.

The beaver is a well known ecosystem engineer and keystone species. It transforms its territory from a stream to a pond or swamp. Beavers affect the environment first altering the edges of riparian areas by cutting down older trees to use for their dams. This allows younger trees to take their place. Beaver dams alter the riparian area they are established in. Depending on topography, soils, and many factors, these dams change the riparian edges of streams and rivers into wetlands, meadows, or riverine forests. These dams have been shown to be beneficial to a myriad of species including amphibians, salmon, and song birds.

In the African savanna, the larger herbivores, especially the elephants, shape their environment. The elephants destroy trees, making room for the grass species. Without these animals, much of the savanna would turn into woodland. In the Amazon river basin, peccaries produce and maintain wallows that are utilized by a wide variety of species. Australian studies have found that parrotfish on the Great Barrier Reef are the only reef fish that consistently scrape and clean the coral on the reef. Without these animals, the Great Barrier Reef would be under severe strain.

Limitations

Although the concept of the keystone species has a value in describing particularly strong inter-species interactions, and for allowing easier communication between ecologists and conservation policy-makers, it has been criticized by L. S. Mills and colleagues for oversimplifying complex ecological systems. The term has been applied widely in different ecosystems and to predators, prey, and plants (primary producers), inevitably with differing ecological meanings. For instance, removing a predator may allow other animals to increase to the point where they wipe out other species; removing a prey species may cause predator populations to crash, or may allow predators to drive other prey species to extinction; and removing a plant species may result in the loss of animals that depend on it, like pollinators and seed dispersers. Beavers too have been called keystone, not for eating other species but for modifying the environment in ways that affected other species. The term has thus been given quite different meanings in different cases. In Mills's view, Paine's work showed that a few species could sometimes have extremely strong interactions within a particular ecosystem, but that does not automatically imply that other ecosystems have a similar structure.

Flagship species

In conservation biology, a **flagship species** is a species chosen to raise support for biodiversity conservation in a given place or social context. Definitions have varied, but they have tended to focus on the strategic goals and the socio-economic nature of the concept, to support the marketing of a conservation effort. The species need to be popular, to work as symbols or icons, and to stimulate people to provide money or support.

Species selected since the idea was developed in 1980s include widely recognised and charismatic species like the black rhinoceros, the Bengal tiger, and the Asian elephant. More locally significant species like the Chesapeake blue crab and the Pemba flying fox have suited a cultural and social context.

Utilizing a flagship species has limitations. It can skew management and conservation priorities, which may conflict. Stakeholders may be negatively affected if the flagship species is lost. The use of a flagship may have limited effect, and the approach may not protect the species from extinction: all of the top ten charismatic groups of animal including tigers, lions, elephants and giraffes are endangered.

The term flagship is linked to the metaphor of representation. In its popular usage, flagships are viewed as ambassadors or icons for a conservation project or movement. The geographer Maan Barua noted that metaphors influence what people understand and how they act; that mammals are disproportionately chosen; and that biologists need to come to grips with language to improve the public's knowledge of conservation. Several definitions have been advanced for the flagship species concept and for some time there has been confusion even in the academic literature. Most of the latest definitions focus on the strategic, socio-economic, and marketing character of the concept.

- "a species used as the focus of a broader conservation marketing campaign based on its possession of one or more traits that appeal to the target audience".
- "species that have the ability to capture the imagination of the public and induce people to support conservation action and/or to donate funds".
- "popular, charismatic species that serve as symbols and rallying points to stimulate conservation awareness and action".

History

The flagship species concept appears to have become popular around the mid 1980s[1] within the debate on how to prioritise species for conservation. The first widely available references to use the flagship concept applied it to both neotropical primates and African elephants and rhinos, in the mammal-centric approach that still dominates how the concept is used. The use of flagship species has been dominated by large bodied animals, especially mammals, although members of other taxonomic groups have occasionally been used.

Flagship species projects have sometimes been successful in saving the species and its habitat, as with the American bald eagle and the manatee.

Choosing species

Chosen flagship species include the Bengal tiger (*Panthera tigris*), the giant panda (*Ailuropoda melanoleuca*), the Golden lion tamarin (*Leontopithecus rosalia*), the African elephant (*Loxodonta sp.*) and Asian elephant (*Elephas maximus*). However, because flagship species are selected according to the audience they are hoping to influence, these species can also belong to traditionally uncharismatic groups, if the cultural and social content is right. Less charismatic but locally significant species include the use of the Pemba flying fox as a flagship in Tanzania, and of the Chesapeake blue crab as a flagship in the USA.

Some flagship species are keystone species, like the African lion, a top predator: it used to control the populations of large herbivores, protecting ecosystems across the entire landscape. However, the lion's ability to serve as a keystone species is decreasing as its population and

range decline. The WWF uses flagship species as one of its species classification categories, along with keystone and indicator species. It chooses between these when selecting a priority species to represent the conservation threats facing a certain region.

Flagship species can represent an environmental feature (e.g. a species or ecosystem), cause (e.g. climate change or ocean acidification), organization (e.g. NGO or government department) or geographic region (e.g. state or protected area).

Flagship species can be selected according to many different methodologies, such as social marketing, environmental economics, and conservation biology, depending on what is valued by the audience they try to target, and the goals of the project, such as conservation awareness, fundraising, ecotourism promotion, community-based conservation, and promotion of funded research. This is illustrated by the differences in recommendations made for flagship species selection targeting different target audiences such as local communities and tourists.

Limitations

The use of flagship species has some limitations:[22]

- They can skew the management and conservation priorities in their favour, to the detriment of more threatened but less charismatic species.
- The management of different flagships can conflict.
- The disappearance of the flagship can have negative impacts on the attitudes of the conservation stakeholders.
- They may have limited impact on the behaviour of donors, if the donors cannot dedicate much time to processing the campaign message.

Leaving aside the impact on other species, charisma does not seem to protect even charismatic species against extinction. All ten of the most charismatic groups of animal identified in a 2018 study, namely tiger, lion, elephant, giraffe, leopard, panda, cheetah, polar bear, wolf, and gorilla, are currently endangered; only the giant panda shows a demographic growth from an extremely small population. The researchers suggest that the widespread use of images of these animals has given the public the impression that the animals are abundant, obscuring their high risk of imminent extinction. They note that this remains true despite the intense focus of conservation efforts on these particular species. A major challenge for the utilization of several flagship species in non-Western contexts is that they may come into conflict with local communities, thereby jeopardizing well-intended conservation actions. This has been termed 'flagship mutiny', and is exemplified by the Asian elephant in countries where there is human-elephant conflict.

Other types

Conservation flagships can be used at broader levels, for example as ecosystems like coral reefs, rainforests or protected areas like the Serengeti or Yellowstone. Some recent initiatives have developed flagships based on the conservation value of particular areas or species. Examples of these are the EDGE project run by the Zoological Society of London and the Hotspots run by Conservation International. More recently, work in microbiology has started to use flagship species in a distinct way. This work relates to the biogeography of micro-organisms and uses

particular species because "eyecatching "flagships" with conspicuous size and/or morphology are the best distribution indicators".

Keystone and Flagship species

A keystone species is an organism that helps define an entire ecosystem. Without its keystone species, the ecosystem would be dramatically different or cease to exist altogether.

Keystone species have low functional redundancy. This means that if the species were to disappear from the ecosystem, no other species would be able to fill its ecological niche. The ecosystem would be forced to radically change, allowing new and possibly invasive species to populate the habitat.

Any organism, from plants to fungi, may be a keystone species; they are not always the largest or most abundant species in an ecosystem. However, almost all examples of keystone species are animals that have a huge influence on food webs. The way these animals influence food webs varies from habitat to habitat.

Carnivores, Herbivores, and Mutualists

Predators

A keystone species is often, but not always, a predator. Just a few predators can control the distribution and population of large numbers of prey species.

The entire concept of keystone species was founded on research surrounding the influence of a marine predator on its environment. American zoology professor Robert T. Paine's research showed that removing a single species, the *Pisaster ochraceus* sea star, from a tidal plain on Tatoosh Island in the U.S. state of Washington, had a huge effect on the ecosystem. *Pisaster ochraceus*, commonly known as purple sea stars, are a major predator of mussels and barnacles on Tatoosh Island. With the sea stars gone, mussels took over the area and crowded out other species, including benthic algae that supported communities of sea snails, limpets, and bivalves. Lacking a keystone species, the tidal plain's biodiversity was cut in half within a year.

Another example of a predator acting as a keystone species is the presence of gray wolves in the Greater Yellowstone Ecosystem. The Greater Yellowstone Ecosystem (GYE) is an enormous and diverse temperate ecosystem stretching across the boundaries of the U.S. states of Montana, Wyoming, and Idaho. The GYE includes active geothermal basins, mountains, forests, meadows, and freshwater habitats.

The elk, bison, rabbit, and bird species in the Greater Yellowstone Ecosystem are at least partly controlled by the presence of wolves. The feeding behavior of these prey species, as well as where they choose to make their nests and burrows, are largely a reaction to wolf activity. Scavenger species, such as vultures, are also controlled by the wolf activity.

When the U.S. government designated land for Yellowstone National Park in the late 19th century, hundreds of wolves roamed the GYE, preying primarily on abundant herds of elk and bison. Fearing the wolves' impact on those herds, as well as local livestock, governments at the

local, state, and federal level worked to eradicate wolves from the GYE. The last remaining wolf pups in Yellowstone were killed in 1924.

This started a top-down trophic cascade in the Greater Yellowstone Ecosystem. A trophic cascade describes changes in an ecosystem due to the addition or removal of a predator. A top-down trophic cascade describes changes that result from the removal of an ecosystem's top predator. (A bottom-up trophic cascade describes changes that result from the removal of a producer or primary consumer.)

Lacking an apex predator, elk populations in Yellowstone exploded. Elk herds competed for food resources, and plants such as grasses, sedges, and reeds did not have time or space to grow. Overgrazing influenced the populations of other species, such as fish, beaver, and songbirds. These animals rely on plants and their products—roots, flowers, wood, seeds—for survival.

The physical geography of the Greater Yellowstone Ecosystem was also impacted by the loss of wolves and subsequent elk overgrazing. Stream banks eroded as wetland plants failed to anchor valuable soil and sediments. Lake and river temperatures increased as trees and shrubs failed to provide shaded areas.

Starting in the 1990s, the U.S. government began reintroducing wolves to the Greater Yellowstone Ecosystem. The results have been noteworthy. Elk populations have shrunk, willow heights have increased, and beaver and songbird populations have recovered.

Herbivores

Herbivores can also be keystone species. Their consumption of plants helps control the physical and biological aspects of an ecosystem.

In African savannas such as the Serengeti plains in Tanzania, elephants are a keystone species. Elephants eat shrubs and small trees, such as acacia, that grow on the savanna. Even if an acacia tree grows to a height of a meter or more, elephants are able to knock it over and uproot it. This feeding behavior keeps the savanna a grassland and not a forest or woodland.

With elephants to control the tree population, grasses thrive and sustain grazing animals such as antelopes, wildebeests, and zebras. Smaller animals such as mice and shrews are able to burrow in the warm, dry soil of a savanna. Predators such as lions and hyenas depend on the savanna for prey.

Keystone Mutualists

Keystone mutualists are two or more species that engage in mutually beneficial interactions. A change in one species would impact the other, and change the entire ecosystem. Keystone mutualists are often pollinators, such as bees. Pollinators often maintain gene flow and dispersal throughout widespread ecosystems.

In the woody grasslands of Patagonia (at the southern tip of South America) a species of hummingbird and indigenous plants act together as keystone mutualists. Local trees, shrubs, and flowering plants have evolved to only be pollinated by *Sephanoides sephanoides*, a hummingbird known as the green-backed firecrown. Green-backed firecrowns pollinate 20% of local plant species. In turn, these plants provide the sugary nectar that makes up most of the hummingbird's diet.

Pockets of the existing Patagonian habitat would collapse without green-backed firecrowns, because their functional redundancy is nearly zero—no other pollinator has adapted to pollinate these plants.

Other Organisms Crucial to Ecosystems

In addition to keystone species, there are other categories of organisms crucial to their ecosystems' survival.

Umbrella Species

Umbrella species are often conflated with keystone species. Both terms describe a single species on which many other species depend. The key distinction between umbrella species and keystone species is that the value of an umbrella species is tied to its geographic species range.

Umbrella species have large habitat needs, and the requirements of that habitat impact many other species living there. Most umbrella species are migratory, and their range may include different habitat types.

The identification of an umbrella species can be an important aspect of conservation. The minimum species range of an umbrella species is often the basis for establishing the size of a protected area.

The Siberian tiger, an endangered species, is an umbrella species with a range of more than 1,000 kilometers (620 miles) in Russia's far east, with territory stretching into China and North Korea. The species range includes heavily forested ecosystems in both temperate and boreal (subarctic) biomes. Populations of deer, boar, and moose are under the snowy "umbrella" of the Siberian tiger range.

Foundation Species

Foundation species play a major role in creating or maintaining a habitat.

Corals are a key example of a foundation species across many islands in the South Pacific Ocean. These tiny animals grow as a colony of thousands and even millions of individual polyps. The rocky exoskeletons of these polyps create enormous structures around islands: coral reefs.

Coral reefs are one of the most vibrant and biologically diverse ecosystems on the planet. Microscopic plankton, as well as crustaceans, mollusks, sponges, fish, and marine reptiles and mammals, are all part of healthy coral reef ecosystems.

Coral reef ecosystems also contribute to the human geography of a region. Pummeled by waves and ocean currents, coral exoskeletons can experience bioerosion. These eroded fragments of coral (along with bony fragments of organisms such as foraminifera, mollusks, and crustaceans) create a soft sand known as coral sand. Coral sand beaches are among the most popular tourist destinations in the world.

Ecosystem Engineers

Like foundation species, ecosystem engineers contribute to the physical geography of their habitat. Ecosystem engineers modify, create, and maintain habitats.

Ecosystem engineers modify their habitats through their own biology or by physically changing biotic and abiotic factors in the environment.

Autogenic engineers modify their environment by modifying their own biology. Corals and trees are autogenic engineers. As they grow, they are a living part of the environment, providing food and shelter to other organisms. (The hard exoskeletons left as corals die, continue to define and modify the ecosystem.)

Allogenic engineers physically change their environment from one state to another. Beavers are a classic example of allogenic engineers. Beavers help maintain woodland ecosystems by thinning out older trees and allowing young saplings to grow. Converting these trees into timber for dams radically alters woodland meadows and streams, changing them into wetland habitats.

Invasive species are often ecosystem engineers. Lacking natural predators or abiotic factors to constrain them, these introduced species modify the existing environment in ways that inhibit the growth of the indigenous ecosystem.

Kudzu, the so-called “vine that ate the South,” is an invasive species of plant that modified the environment of the southeastern United States. Kudzu regularly outcompetes native species for space and nutrients. As it crowds out native species, kudzu limits the pollinators, insects, and bird species that inhabit an area.

Indicator Species

An indicator species describes an organism that is very sensitive to environmental changes in its ecosystem. Indicator species are almost immediately affected by changes to the ecosystem and can give early warning that a habitat is suffering.

Changes associated with external influences such as water pollution, air pollution, or climate change first appear in indicator species. For this reason, indicator species are sometimes known as “sentinel species.”

In the “nation’s estuary” of the Chesapeake Bay, oysters are an indicator species. Oysters and other bivalves are filter feeders, meaning they filter water as they strain it for food particles. Oysters filter nutrients, sediments, and pollutants that enter the bay through natural or anthropogenic sources. Oyster beds help protect fisheries, coastal habitats, and even benthic ecosystems. The health of oyster populations in the Chesapeake, therefore, is used to indicate the health of the entire ecosystem.

Flagship Species

A flagship species acts as a symbol for an environmental habitat, movement, campaign, or issue. They can be mascots for entire ecosystems.

The identification of a flagship species relies heavily on the social, cultural, and economic value of a species. They are often “charismatic megafauna,”—large animals with popular appeal due to their appearance or cultural significance. Flagship species may or may not be keystone or indicator species.

Flagship species can sometimes be symbols of general ideas about conservation, not representatives of specific ecosystems. However, specific issues are often associated with a specific animal. The movement to end seal hunting in the Arctic found its flagship species in the juvenile harp seal. Polar bears are the unchallenged flagship species associated with climate change.

The giant panda is perhaps the most familiar flagship species. Pandas are the global symbol of endangered species and the value of captive breeding.