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### “Keystone Species”

In a short note published in 1969, Robert T. Paine proposed that some carnivorous species that maintain the integrity and persistence of a community through time are “keystone species”. He based this proposal on his own documentation of positions in the food web (trophic pathways) in intertidal marine communities in the Gulf of California and on the open coast of Washington (Paine 1966). In both cases sea stars were the top predators that he considered to be keystone species. In 1974 Paine published the results of experiments supporting his proposal. At his study site in Washington, he manipulated the abundance of ochre sea stars (*Pisaster ochraceus*). These sea stars preferentially prey on mussels (*Mytilus californianus*), the major space holders in the community. When sea stars were removed, mussels expanded to lower levels in the intertidal, displacing other species (for example, barnacles and algae) attached to the rocks. Consequently, the community was completely changed from one with a wide variety of species attached to the rocks to one dominated by mussels and the many species living within the mussel bed. Similar experiments with sea stars in New Zealand resulted in similar expansion of mussel beds, making these observations general (Paine 1971) and supporting the idea that a predator at the top of a food web controlled community structure and function.

James A. Estes and James F. Palmisano (1974) consolidated the keystone species idea with their work in the Aleutian Islands, where sea otters were expanding their range after being nearly exterminated a century earlier by the fur trade. They found that on islands where sea otters were present there was a diverse kelp forest community. On the other hand, on islands where the sea otters had not returned, the sea floor was carpeted with sea urchins with almost no algae. They saw sea otters as a keystone species that, by preying on sea urchins, allowed a complex kelp forest community to thrive. A healthy kelp forest community is home to many other species including fishes. The community, in turn, supports eagles and other species beyond the kelp forest.

While sea stars and sea otters became the iconic keystone species, other top predators such as lions, wolves, foxes, bass, and even humans entered the list. Keystone species became nearly any species that had a particularly strong impact on a community, and as such the concept became rather imprecise and fuzzy. There was much discussion ensued ecologists (e.g., Simberloff 1991, Mills et al. 1993, Menge et al. 1994, Paine 1996). Eventually a group of ecologists met and expanded Paine’s (1969) original usage of the term, which had focused on species that preferentially consumed and limited other species that could dominate a community. They defined a keystone species “... as one whose impact on its community or ecosystem is large, and **disproportionately** large relative to its abundance” (Power et al. 1996). With this definition a keystone species can exert its effect on a dominant species not only by consumption, but also by things like competition, mutualism, dispersal, pollination, disease, or by modifying habitats or non-biological factors. Specific flowers that are central to maintaining pollinators,

for example, can be considered keystones, as can lichens that break down rocks to create soil, or bacteria that fix nitrogen. All these species can have a large effect on a community relative to their abundance. If they are removed, the community changes dramatically in its organization, structure, and species composition, although not necessarily in species diversity.

The keystone species definition developed by Power et al. (1996), while still rather ambiguous, is now widely accepted by ecologists (e.g., Jordán 2009, Cottee-Jones 2012). The concept has even been extended to species that characterize human cultures (“cultural keystone species”)(Garibaldi and Turner 2004), although not without pushback (Nuñez and Simberloff 2005). There are now many species recognized as keystones, but ochre sea stars were the first and they remain the celebrity keystone species.

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