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Bio 602-Ecological thought past and present
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Discussion topic proposal: Keystone Species

A keystone species is defined by Power et al. as "one whose effect is large and disproportionately large relative to its abundance" (1996). With a field as diverse and sprawling as ecology it can be difficult to identify principles (and specific studies addressing those principles) that can engender productive, coherent, and useful discussion sessions. At the risk of sounding overly contrite (even for a scientist attempting to come up with a catchy punchline for a project proposal) I believe that keystone species will make for a great keystone topic of discussion. The first discussion session will cover the first set of studies (Paine, 1966; 1969) to explicitly address the keystone species concept along with a review paper (Power et al., 1996) that redefines the keystone species concept, synthesizes the results of studies from previous decades, and points to important future research questions to be addressed. The current study (Letnic et al., 2009) displays the power of the keystone species concept both in explaining basic ecosystem function and helping to make better informed conservation decisions.

The study conducted by Paine (1966) in three geographically distinct intertidal communities is impressive (for its time) in its breadth and its experimental approach, using both manipulative and observational approaches. The study documented 'subweb' (simplified food web) structure in a tropical, temperate, subtropical and intertidal hard bottom communities. Each community type had different numbers of trophic levels within its subwebs (tropical = 2, temperate = 3, subtropical = 5) with higher numbers of trophic levels corresponding to greater community wide diversity within each subweb.

The apparent relationship between trophic complexity and diversity was verified by removing an apex predator, the starfish *Pisaster spp.* from the temperate intertidal zone and observing how the composition of the community changed over time. The community decreased from 15 members to 8 members and sponges, nudibranchs, and anemones (which were not part of the subweb being studied) also disappeared from the community. The author hypothesized that removal of *Pisaster spp.* released barnacles from grazing pressure which allowed them to competitively exclude other sessile invertebrates. Therefore the study demonstrated the role of *Pisaster spp.* as keystone species in the temperate communities, and indicated the likely mechanism that resulted in the positive relationship between trophic complexity and diversity.

The same mechanism of top down control acting in rocky intertidal communities is proposed to function in Australian reef community in Paine (1969). This short note poses the hypothesis that harvesting of the triton *Charonia spp.* by the tourist industry released the corrallivorous starfish *Acanthaster spp.* from control resulting in decimation of the reef. This paper appears prescient given the important role that the keystone species concept plays in making conservation decisions today.

The review by Power et al., 1996 is co-authored by the same Paine who performed the early work addressing the keystone species concept, so it provides a nice demonstration of how the intellectual seeds of the keystone species concept as put forth in Paine's early work matured over the intervening decades. By defining keystone specie(s) as "those whose effect(s) are large and disproportionately large relative to its (their) abundance" the authors differentiate dominant species such as trees (which have effects that are proportional to their abundances) with keystone species such as sea otters or predatory whelks. The definition put forth by the authors is formalized in mathematical terms as a measure of community importance (CI), which is a function of the ecosystem effect a given species has on a particular ecosystem characteristic (productivity, space, biomass) relative to the biomass or number of individuals present. Although consumption is often identified as a mechanism by which keystone species exert their influence it is important to focus increased attention on other important potential mechanisms that are less studied such as disturbance, disease effects, and resource partitioning.

Given their potentially critical role in threatened ecosystems there is great interest in identifying traits that characterize keystone species to facilitate their rapid identification. This has been difficult so far for several reasons, namely, that the keystone status of a species often appears to be context dependent, and may change with successional status, productivity, diversity, and other ecosystem traits. Therefore it is important to identify how the importance of traits that define keystone species change across a gradient of conditions. This functional-trait focus in conservation contrasts with the previous focus on using species-rarity and biodiversity as the primary criteria for conservation decisions, and has the potential to allow for more efficient allocation of time and resources when attempting to preserve functions of threatened ecosystems as was discussed in our readings on the ecosystem effects of biodiversity.

The reading by Letnic et al. provides an example of how the keystone species concept may be valuable in progressing basic scientific discovery and making applied management decisions, all over the course of one study. The study demonstrates the keystone function of an apex predator (the dingo *Canus lupus dingo*) and quantifies how changing management of this predator might impact threatened lower trophic level animals through a trophic cascade, (2009). In a world where species invasions are increasingly common and management efforts are increasingly directed towards preventing the spread of invasives and controlling their spread this paper provides an interesting counterpoint. The keystone apex predator whose beneficial ecological effects the paper demonstrates is also an invasive.

Removal of apex predators may free lower trophic level predators (mesopredators) from control by predation, which may in turn have negative effects on the prey of mesopredators. This cascade of trophic effects is termed the mesopredator release hypothesis (MRH). Dingos were almost completely eliminated from a large section of southeastern Australia to prevent them from preying upon livestock in this area. Populations outside this area were prevented from reentering using an exclusion fence. According to MRH elimination of dingos might remove invasive foxes and feral cats from predation pressure thus increasing predation pressure on small threatened native prey species and decreasing predation pressure on large herbivorous livestock and kangaroos, thus negatively affecting grasses. When dingos were present it was expected that rabbits, small mammals and grasses would be positively affected. To test this hypothesis community composition, trophic dynamics, and environmental factors were measured at eight sites, each containing two subsites, with one subsite on either side of the dingo exclusion fence.

The abundance of apex predators and mesopredators, larger herbivores, and small herbivores at each site was assessed using track stations, spotlight transects, and pitfall traps, respectively. Vegetation cover at each site was measured and grazing intensity was assessed by measuring the amount of herbivore scat present at each site. Predation pressure was assessed and trophic dynamics were investigated by measuring the abundance and composition of scat from predators at each site. A model was created to estimate the potential effect on small threatened mammals of releasing dingos back into the exclusion area.

As expected dingos were more common outside the fence and foxes and cats were the most common inside the fence. In agreement with MRH the absence of dingoes had negative effects on abundance foxes and kangaroos and positive effects on abundance and species richness of small mammals and grass cover. Surprisingly the absence of dingos did not affect the abundance of rabbits or cats. The model used to estimate the net effect of dingo absence on threatened small mammals predicted net positive effects would occur in 82.6 percent of the area considered and net negative effects would occur in 2.4 percent of the area.

The results of the study provided initial support of the MRH in the areas studied. However, it had important limitations in that the study was a non-manipulative snapshot type experiment. There is strong indication that mechanisms involved in MRH are acting to create the patterns observed but manipulative experiments are necessary to verify that these mechanisms are in play. It is possible that interactive effects resulting from changing fox, kangaroo, and grass abundances in the absence of dingos may have produced the patterns observed. It is also unclear why rabbits and cats did not respond to dingo removal. Rabbits in sand dune biomes were more abundant in the presence of dingos but when all biomes were considered this was not the case suggesting the relationship may be context dependent. It is possible that because dingos and foxes both consume rabbits and cats and that rabbit and cat population levels may be more dependent on other factors such as rainfall.

The keystone species concept clearly has an important place in basic and applied ecological theory in its own right. Due to the strong interactive effect keystone species may have on multiple components of the ecosystem their effects may be wide ranging and occur on different scales. Therefore a discussion of this topic might provide an ideal forum to synthesize ideas which have been discussed in previous topic discussions.

Literature cited

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