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Editorial

Keystones to sustain life's diversity

A little over 50 years ago, Robert Paine, at that time resembling a dashing Robert Redford (Power *et al.* 2018), gave community ecology a concept that has proved its relevance time and time again. Paine was studying rocky shore marine communities off the west coast of Washington State, near Vancouver. He found and demonstrated experimentally that the predatory purple starfish *Pisaster* was responsible for preventing the spatial dominance of the mussel *Mytilus* and thereby ensured the survival of many other rock-dwelling species such as chitons and barnacles. The absence of the starfish led to a trophic collapse in which *Mytilus* largely won the competition for the rocky space, resulting in a community that was much diminished in diversity. Paine termed the purple predator a keystone species, since removal of this species caused the community to collapse, similar to the collapse of a stone arch when the keystone is removed (Paine 1966). In a delightful and thought-provoking conversation between Dr. Knowitall, Empiricist and Skeptic, Paine (1995) further refined the keystone concept: "As George Orwell noted, some pigs are more equal than others, and the same applies to all species."

Over the years, this concept has been suggested as an explanation for the survival of diverse species in several communities, but unlike Paine's heroic removal experiments in which he physically cleared *Pisaster* from sites, few empiricists have been able to conduct such experiments in natural settings and demonstrate the keystone nature of particular taxa. However, their keystone value is usually implicit. For example, figs are considered a keystone species because they provide fruit to frugivores during periods of general fruit scarcity in a tropical forest when all other tree species are barren (Lambert and Marshall 1991). This functional trait is a consequence of continual fig fruit production resulting from their peculiar pollination system in which figs breed their own wasp pollinators in their unripe fruit. The absence of fig trees in a fruit tree community may result in reduction of fruit availability during critical general fruit shortages and thereby result in the shrinkage or alteration of frugivore diversity at a particular location.

Can genes have 'keystoneness'? Can the presence or absence of certain genes within species alter the species composition of a trophically connected community? This has been speculated and candidate genes with a disproportionately large effect on communities have been putatively identified (Skovmand *et al.* 2018). *Bt* genes that have been artificially inserted into transgenic plants have been suggested to affect ecosystems (Rossi-Marshall *et al.* 2007). Recently, a keystone gene with an impact on species diversity of an artificially constructed experimental community has been reported (Barbour *et al.* 2022). A simple food web with *Arabidopsis* at the base was constructed. Two aphid species that feed on *Arabidopsis*, one more dominant than the other, and a parasitoid wasp whose larvae prey upon both aphid species formed the rest of the food web. This experimentally constructed food web, therefore, had *Arabidopsis* as the primary producer, the aphids as herbivores, and the wasps as predators, forming a trophic pyramid. *Arabidopsis* defends itself against herbivores by the synthesis of glucosinolates; however, the production of chemical defences comes at the cost of growth (Züst *et al.* 2012); those *Arabidopsis* varieties with functional genes in the glucosinolate pathway produce less biomass and thereby provide less food for herbivores. Barbour *et al.* constructed several artificial food webs using *Arabidopsis* plants with functional or null alleles of three genes in the glucosinolate pathway, in various combinations. A loss-of-function allele of the *AOP2* gene that normally catalyses the transformation of 4-methylsulfinyl glucosinolate (4MSO) to 3-butenyl glucosinolate (But-3-enyl) resulted in greater growth in *Arabidopsis*, allowing the survival of both the dominant and less dominant aphid species as well as the parasitoid, thereby maintaining the entire food web. Varieties of *Arabidopsis* with a functional *AOP2* gene are able to sustain only the dominant aphid species, resulting in a diminished food web. *AOP2* also has pleiotropic effects, and its non-functional allele therefore may also affect

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plant phenotype in different ways. While the impacts of the two other genes and their null versions were tested, only the null *AOP2* allele was identified as a keystone gene.

How would the three conversationalists conjured by Paine react to these results? Empiricist would crowingly say that the careful combinatorial genetic backgrounds and experimental set-ups allowed the keystone gene concept to be validated. Skeptic would be pursing her lips, and Dr Knowitall would probably have a wry smile.

The keystone concept has serious consequences for the long-term survival of biological diversity. Identifying keystones is important to be able to predict the loss of which species would have a greater differential impact on ecosystems (Power *et al.* 1996). The matter is particularly urgent in the Anthropocene, where the Sixth Extinction Event has already claimed many species, e.g. as much as 13% of all known gastropods (twisted shell molluscs) and orders of magnitude higher values than what is known and recorded by IUCN for many groups including the charismatic birds and mammals (Cowie *et al.* 2022). Henrik Österblom, Director of the Stockholm Resilience Centre at Stockholm University, has invoked the keystone species concept in the context of innovative ocean governance (Österblom 2017) and believes that science and business can collaborate for sustained ocean stewardship (Österblom *et al.* 2017). There are undoubtedly hiccups in this collaborative process, and transnational forces are pulling in different directions, with some more powerful than others (Virdin *et al.* 2021); in this commercial ecosystem, too, keystone values need to be preserved to allow smaller businesses to flourish.

There is merit in uncovering the cogs and wheels of ecosystem functioning. The early human Neolithic cultures discovered the importance of keystones, and some of them are still supporting the cavities or arches of ancient architecture. Humans now need to find and conserve natural keystones, for in them will be contained the blueprints of survival.

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Renee M Borges
Indian Institute of Science, Bangalore, India
(Email, renee@iisc.ac.in)
Editor-in-Chief, Journal of Biosciences