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perspective

The keystone species concept: a critical appraisal

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Abstract. The keystone concept has been widely applied in the ecological literature since the idea was introduced in 1969. While it has been useful in framing biodiversity research and garnering support in conservation policy circles, the terminology surrounding the concept has been expanded to the extent that there is considerable confusion over what exactly a keystone species is. Several authors have argued that the term is too broadly applied, while others have pointed out the technical and theoretical limitations of the concept. Here, we chart the history of the keystone concept's evolution and summarise the plethora of different terms and definitions currently in use. In reviewing these terms, we also analyse the value of the keystone concept and highlight some promising areas of recent work.

Keywords. community composition, ecosystem engineer, definitions, dominant species, keystone concept, keystone species

Introduction: the origins of the concept

The keystone concept has its roots in food-web ecology, and was coined by Paine (1969). In his experimental manipulation of rocky shoreline communities on the Pacific coast in Washington, Paine found that the removal of the carnivorous starfish *Pisaster ochraceus,* the top predator of the local system, led to the local extinctions of several benthic invertebrates and algae (Paine 1966). In a subsequent short note (Paine 1969:92) he used this example, alongside that of the impact of another starfish *Acanthaster planci,* on parts of the Great Barrier Reef, to argue that "the species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time, that is, stability, are determined by their activities and abundance. They may be unimportant as energy transformers." He argued, in effect, that the keystone species had a disproportionate influence on key community properties and explicitly claimed that variation in the abundance of other predators "would produce no impact comparable to that produced by variations in the keystone species" (p. 93). Paine's field experiments have become a classic ecological case study, with his diagrams reproduced in many standard ecology texts, his 1966 paper cited 2,509 times, and his note coining the term 'keystone species' 465 times (ISI Web of Knowledge 13th September 2012). The concept itself has become widely used, with over 1,600 articles using it in their title or to describe their topic (ISI Web of Knowledge 13th September 2012).

Throughout the 1970s and 1980s a range of species were identified as keystone species. In marine ecosystems the sea otter (*Enhydra lutris*) was found to control sea urchin populations along the Aleutian Islands, which maintained littoral and sub-littoral community structure and increased species diversity and primary productivity (Estes & Palmisano 1974). In freshwater ecosystems in North America, beavers (*Castor canadensis*) were found to influence plant and animal community composition and richness in wetland and riparian habitats (Naiman et al. 1986), while in terrestrial ecosystems pocket gophers (Geomyidae) were believed to keep North American prairie soils in a condition that could support higher plant diversity (Huntly & Inouye 1988). The concept was also applied palaeoecologically, with North American megafauna described as ‘keystone herbivores’ that created a mosaic of open woodlands and grasslands during the Pleistocene (Owen-Smith 1987). In policy dialogues the keystone concept was championed by Simberloff (1998), because managing keystone populations was thought to help conserve the populations of other species in protected areas (Carroll 1992, Caro 2010).

Expansion of the keystone concept

While Paine originally intended keystone species to refer to those species that maintained the stability of an ecosystem (like the keystone in an arch), this idea was not retained in the subsequent development of the term. In fact, his reference towards a disproportional relationship between the keystone species and the community was lost in some reconfigurations, while others abandoned the notion of a single species being the keystone. For example, Gilbert (1980) proposed that plants which provide critical support to complexes of pollinators and dispersers should be described as keystone mutualists, which if lost from an ecosystem would lead to a collapse in functionality and species richness. The idea of ecological collapse was then developed by Terborgh (1986), who argued that, in Neotropical forest ecosystems at least, a handful of keystone plant resources were critical to providing food for frugivores during the fruit-scarce dry season, and so set the carrying capacity of the community. He suggested that a reduction in frugivore populations would follow the removal of such keystone plant resources, and the subsequent loss of seed-dispersal pathways in the forest would result in a decrease in species richness through a cascade of extinctions.

While the keystone concept became popular in both research and policy arenas, it was not without its critics. For example, Mills et al. (1993:219) argued that the term was “broadly applied” and “poorly defined” and that basing conservation strategies on keystone species was dangerous. Indeed the evolution of terminological confusion, which Peters (1988) described for food-web ecology, could just as easily be applied to the keystone concept (see Figure 1).

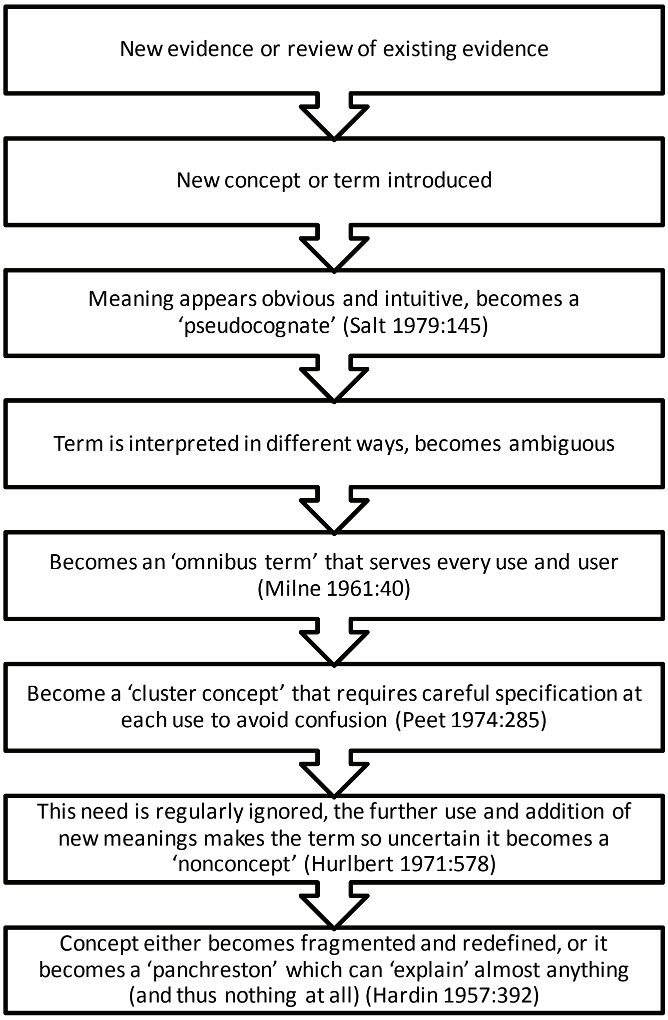

Figure 1. The demise of a scientific term (following Peters 1988).

In response to the challenge of identifying keystone species more precisely, a small conference was held in Hilo, Hawaii (8–11 December 1994), where international policy practitioners and ecologists who had worked on the keystone concept attempted to produce a consensus definition of a keystone species. They agreed on the following definition: “a keystone species is a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance” (Power & Mills 1995:184) and published a paper the following year where they attempted to identify the magnitude of the influence one species has on its community, known as its ‘community importance’ (Power et al. 1996).

Despite this attempt to pin down a definition of keystone species and produce a tool to identify species that fit the consensus definition, confusion still surrounds the term (Piraino & Fanelli 1999, Barua 2011). This may be because: 1) the definition from Hilo retains a large degree of ambiguity; and 2) the community importance tool remains incomplete, with no quantitative threshold to determine the level of community importance needed to gain keystone status. Nonetheless, researchers continue to apply the concept to an ever-growing number of species and scenarios. For example, in 2010 and 2011 the Nile Crocodile (*Crocodylus niloticus*), Black Woodpecker (*Dryocopus martius*), European Rabbit (*Oryctolagus cuniculus*), Plateau Pika (*Ochotona curzoniae*), a parasitic fungus (*Ophiocordyceps unilateralis*), a species of Japanese bamboo grass (*Sasamorpha borealis*), the Brown Bear (*Ursus arctos*), Grey Wolf (*Canis lupus*), Eurasian Lynx (*Lynx lynx*), Black-tailed Prairie Dog (*Cynomys ludovicianus*), Bearded Goby (*Taenioides jacksoni*) and a squid (*Loligo plei*) were all described as keystone species (Ashton 2010, Gasalla et al. 2010, Konsinski et al. 2010, Moloney 2010, Delibes-Mateos et al. 2011, Evans et al. 2011, Magle & Angeloni 2011, Tsuyama et al. 2011, Ucarli 2011). While the high number of species identified as keystones does not mean they are inaccurate, different definitions are being applied, resulting in a lack of consistency in the criteria used to assign keystone status. For example, the European Rabbit was awarded keystone status because of the disproportionate effect it has on community function relative to abundance (Delibes-Mateos et al. 2011), while the Bearded Goby was given keystone status because it plays a "unique ecological role" on the Namibian continental shelf (Moloney, 2010:5). This list further reflects the three main

Keystone species definitions (adapted)	**Reference**
Definitions involving a strong influence	
A species whose population is "the keystone of the community's structure", whereby the integrity and stability of the community are determined by its activities and abundance.	Paine 1969:92
"Keystone species are those whose removal from a community would precipitate a further reduction in species diversity or produce other significant changes in community structure and dynamics."	Daily et al. 1993:592
"Keystone species play a critical role in determining community structure."	Jones et al. 1994:380
"Relatively rare species in a community whose removal causes a large shift in the structure of the community and the extinction of some species."	Krebs 2009:378
"Rare species of low abundance in a community but whose removal has drastic effects on many other species in the community."	Krebs 2009:402
Definitions involving a disproportionate effect relative to abundance	
Species which "have a disproportionate effect on the persistence of all other species."	Bond 1993:236
"A species whose impacts on its community or ecosystem are large and greater than would be expected from its relative abundance."	Heywood 1995:290
A species "whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance."	Power et al. 1996:609
"Consumers having a disproportionately large effect on communities and ecosystems."	Menge & Freidenburg 2001:622
Definitions involving a disproportionate effect relative to biomass	
A species which has "impacts on many others, often far beyond what might have been expected from a consideration of their biomass or abundance."	Simberloff 1998:254
"A species that has a disproportionate effect on its environment relative to its biomass. Such organisms typically have a strong influence on many other organisms within an ecosystem and may play an important role in determining the structure of the ecological community."	Ladle & Whittaker 2011:261

Table 1. A selection of published definitions for the term 'keystone species'.

problems with the definition of keystone species, namely: 1) there are too many alternative definitions in the literature; 2) the definitions are often vague and imprecise; and 3) the term has been expanded to encompass a range of other ecological relationships (Tables 1 and 2).

The extension of the keystone term to include other elements, such as mutualisms, guilds, etc., further complicates the task of delimiting the meaning of the term (Table 2). If these tables make one thing clear, it is that the number and range of keystone concept definitions has reached unworkable levels, and is in need of refinement. There are two options here: 1) formulate a specific definition of 'keystone', with testable quantitative thresholds, which would allow researchers to discard or include the wealth of species currently listed as keystones; or 2) use a general definition that encompasses the current interpretation of the keystone concept, which can be broadly applied, and which has no quantifiable thresholds or criteria. The first option is preferable, but for reasons discussed below, there are larger theoretical and practical issues that constrain the validity of the keystone concept. Therefore it may be sensible to follow the second option, and propose a general definition that reflects the current use of the keystone idea in scientific, policy, and public settings. So in practice, by reference to the way that the term is used in much of the literature, it would be more defendable to describe the current usage as follows: 'a keystone species is a species that is of demonstrable importance for ecosystem function'. For the variants of the keystone concept, the word species is substituted with the relevant term (for example a key-

Term	Adapted definition	Example	Reference
Keystone Mutualist	"[T]hose organisms, typically plants, which provide critical support to large complexes of mobile links." (Where mobile links are animals required by many plants for reproduction and dispersal).	The canopy tree *Casearia corymbosa* (Howe 1977)	Gilbert 1980:32
Keystone Plant Resource	Those plants which play "prominent roles in sustaining frugivores through periods of general food scarcity."	*Ficus* trees, palm nuts	Terborgh 1986:339
Extended Keystone Hypothesis	"All terrestrial ecosystems are controlled and organized by a small set of key plant, animal, and abiotic processes."	North American forest insect pests (Holling 1986)	Holling 1992:449
Keystone Modifier	Those "species which greatly affect habitat features without necessarily having direct trophic effects on other species."	North American Beaver *Castor canadensis* (Naiman et al. 1986)	Mills et al. 1993:220
Keystone Guild	Where similar species in an ecosystem are "known to have impacts that are disproportionally large relative to their collective biomass."	Flying foxes (*Pteropus* spp.) on Samoa (Elmqvist et al. 1992)	Power et al. 1996:613
Reverse Keystone Species	A species which "must be absent or at very low density if a typical species-rich assemblage...is to be sustained in a local area."	Noisy Miner (*Manorina melanocephala*)	Piper & Catterall 2003:609
Cultural Keystone Species	"Those plant and animal species whose existence and symbolic value are essential to the stability of a culture over time."	Cocoa in various indigenous Amazonian communities	Cristancho & Vining 2004:153
Keystone Structure	Ecological structures which "exert a disproportionate effect on ecosystem function in a wide range of ecosystems", the loss of which "may lead to the deterioration of important ecosystem functions."	Dehesas scattered tree landscapes in Spain and Portugal (Díaz et al. 1997)	Manning et al. 2006:311, Tews et al. 2004

Table 2. Other variants of the keystone concept and their definitions.

stone structure would be a structure that is of demonstrable importance for ecosystem function). This abandons the notion of proportion that existed in earlier definitions, and moves away from the original idea of ecosystem stability. It also gives practitioners and the public a common reference point which conveys the central message it is believed to carry, and perhaps more importantly, it does not give any false illusions of being a precise scientific term.

Theoretical and practical constraints to providing a precise definition of 'keystone'

The idea of proportionality, where a keystone species had to have a disproportionate influence on its community relative to either its abundance or biomass, introduced a great deal of uncertainty into the concept, without necessarily being well grounded biologically (Mills et al. 1993). In order to identify a keystone species, it meant that all the individuals of all species in a community had to be counted, or that the biomass of the suspected keystone species had to be compared in relative terms to the biomass of the entire community. While both conditions are extremely difficult to satisfy in practice, the vast majority of species are likely to have a very small biomass relative to their entire community, and so with this clause most species, and almost every top predator, could be described as a keystone species.

While this attempted re-definition may just confirm that the keystone concept has become a panchreston, where it is so vague that it can 'explain' almost anything (Hardin 1957:392), it at least avoids the complications of proposing a more quantifiable, precise definition – which is difficult to defend because such implementations of the keystone concept are almost impossible to test. This general definition also avoids the debate over whether keystone species should maintain species richness, community structure, productivity or nutrient cycling pathways, by emphasising ecosystem function instead. This updates keystone theory from its original reference to ecosystem stability, which lacks empirical support in many natural or semi-natural systems. Instead, a focus on ecosystem processes aligns the keystone concept with biodiversity conservation and the idea of functional resilience, defined as the amount of disturbance an ecosystem can withstand "without changing self-organised processes and structures" (Gunderson 2000:425).

Returning to the genesis of the concept, in Paine's (1966) study the scientific basis for his claim was rather limited, which leads one to question the validity of *Pisaster ochraceus* as a keystone species, even in the terms of the original definition. Paine's field site was an eight metre-long fragment of shoreline in Mukkaw Bay, Washington State, and the only species removed from the experimental area was *P. ochraceus*. There were no neighbouring experiments where other species were excluded and there was no replication. Rather, Paine (1969:92) wrote that "indirect evidence strongly suggests that equivalent changes do not appear with the exclusion of other consumers." Furthermore, when Menge and colleagues conducted experiments on other areas of the Pacific coast in Oregon, they found that *P. ochraceus* only played an important role in wave-exposed sites, and so this particular starfish did not merit keystone status more generally across space (Menge et al. 1994).

The second case study Paine used as evidence for the existence of keystones was from the Great Barrier Reef, Australia. In the 1960s the population of the starfish *Acanthaster planci* reached plague proportions, and was destroying large sections of the reef by feeding on hard corals. At the time, tritons of the *Charonia* genus, which prey on *A. planci*, were being over-exploited by the tourist souvenir industry, and so Paine hypothesised that *Charonia* had been acting as a keystone, holding densities of *A. planci* at low levels and thus preserving a diversity of hard corals. However, *Charonia* snails can only eat about one *A. planci* per week, and so their capacity to control the starfish's population appears limited. Furthermore, the sites of the initial 1962 outbreak did not correspond with the sites that were most visited by tourists; and following their protection in 1969, triton snails are no longer collected, yet there were subsequent outbreaks of *A. planci* in 1979, 1994, and 2003. Instead the fluctuations in

A. planci populations are believed to be the result of a combination of factors, involving other predators such as the Humphead Maori Wrasse (*Cheilinus undulates*) and human influences on the Great Barrier Reef's water quality, where coastal run-off has increased nutrient levels, improving survival rates of *A. planci* larvae (Harriott et al. 2003). The evidence that *A. planci* outbreaks were mediated by the exploitation of a hypothetical keystone in *Charonia* snails was anecdotal in 1969 (Bond 1993), and in light of later work it appears that Paine's assumptions may have been unjustified.

Subsequent attempts to identify keystone species have fallen foul of similar methodological criticisms and overt subjectivity (Mills et al. 1993, Hurlbert 1997), leading to several attempts to formulate a standardised methodology to identify 'keystones'. Power and colleagues divided possible methods into two categories: experimental and comparative (Power et al. 1996). Experimental techniques follow Paine (1966) and involve the exclusion of suspected keystone species from the community. To be thorough, this method should be followed for all species in the community, which leads to logistical difficulties on top of the ethical issues surrounding such experimental manipulation. Further issues over scale effects, both spatially and temporally, ought to be considered, especially given that the demands of excluding species often means that the study site has to be small (Menge et al. 1994, Power et al. 1996, Wootton 1997). The second method, comparative studies, involves comparing two sites with different densities or presence/absence of potential keystone species. Drawing robust conclusions from such analyses is often difficult, however, because confounding factors may mask ecological relationships (Gotelli et al. 2011).

Testing for 'keystones'

While there are problems with both of these methods, there are greater issues in assessing the strength of interactions between a potential keystone and other species in the community. Power and colleagues built on Paine's (1992) 'interaction strength' in developing their community importance index, which measures "the change in a community or ecosystem trait per unit change in the abundance of the species" (Power et al. 1996:609). Their method relied on the experimental approach because of the difficulty in measuring the effects of small changes in abundance, and unlike Paine, who used a per capita measure, Power and colleagues normalised a species' impact by using its proportional biomass. In a recent contribution, which reverts to the per capita approach, Novak and Wootton (2010) developed Paine's 1992 index and Wootton's (1997) dynamic index. In order to scale out differences in population size, they defined the per capita interaction strength between species as the "direct effect that one individual of the first species has on one individual of the second species per unit time" (Novak & Wootton 2010:1057). While they argued that the appropriate experimental interaction strength index is the correct way to test species interactions, they admitted that each index is subject to several assumptions, which often leave empirical ecologists frustrated with theory that cannot readily be applied to natural systems.

In an attempt to avoid the problems of experimental manipulation, Gotelli et al. (2011) employed a comparative statistical methodology that analysed ecological variables in unmanipulated samples. Their method uses randomisation tests to quantify the average effect a particular species' presence or absence within these samples has on a set of ecological variables. In contrast to Power et al. (1996), they avoided scaling their results by abundance or biomass because the measures for rare species would be divided by a small number, greatly inflating the uncertainty and errors in the index (Gotelli et al. 2011:640). While this procedure worked for biological crust communities in central Spain, they found that estimates of species importance were still confounded by particularly strong species interactions, unmeasured abiotic variables, and the reciprocal effects of environmental variables on species presence (Gotelli et al. 2011:634).

Novel approaches to identifying community importance or interaction strength include measuring the unique ecological function that cannot be provided by a different species (Perry 2010), community viability analyses (Ebenman & Jonsson 2005), community sensitivity analyses (Berg et al. 2011) and network analyses (Jordán 2009, Aizen et al. 2012, Lewinsohn & Cagnolo 2012, Pocock et al. 2012). Further exploration of these avenues may offer ways to rank, on a quantitative basis, the importance of a species to a community, and therefore identify a threshold for keystone species, but all have significant obstacles to overcome. Network and sensitivity analyses, for example, rely on simplifying complex ecological relationships, and excluding some effects so that the network size is small enough to analyse. However, aggregating species into groups will lead to inaccuracies, and isolating parts of ecological networks will exclude potentially important external effects (Jordán 2009). These new approaches also still struggle with context dependency in the identification of keystone species, i.e. where a species can be a keystone in one community but not in another very similar community, either across space or over time (Mills et al. 1993, Menge et al. 1994, Christianou & Ebenman 2005). This point has been illustrated in the range of results found in recent network studies, where plants, higher taxonomic families, and interactions rather than organisms were the keystone components in the organisation of three communities (Aizen et al. 2012, Lewinsohn & Cagnolo 2012, Pocock et al. 2012, Stouffer et al. 2012). Until a satisfactory method can be found to determine a threshold for keystone species delimitation, a precise scientific definition will remain elusive.

Alternatives to the keystone concept

The keystone concept is also plagued by issues beyond its own definition and the quantitative identification of keystones. Further terminological confusion is introduced by the overlap of the keystone concept with other terms, such as 'ecological dominant', 'ecosystem engineer' (which is used interchangeably with 'ecological engineer'), and 'foundation species' (Table 3). This has led to the misapplication of each of these terms, as discussed below.

The close links between the 'dominant species' concept and the 'keystone species' concept provide a good example of two terms that can easily become confused. Indeed, we contend that the distinction between the terms is unclear and unresolved and that this owes much to the fact that the two terms originated in different branches of ecology at points separated by around half a century: the dominant species being a product of early 20th century phytosociology and the keystone species being conceived initially by a zoologist examining food-web structures. The plant ecologist F.E. Clements was writing on the role of the dominant around 100 years ago (see Table 3). In short, within his view of the community as a super-organism, the dominants were the species of greatest biomass, which shaped the character of the community and which were diagnostic to the community identity. They were, moreover, crucial to the maintenance of the steady state of the climax community, just as Paine (1969) represented the keystone species as

Term	Adapted definition	Example	Reference
Dominant Species	"The abundant and controlling species of characteristic life-form were long ago termed dominants (Clements 1907; 1916), this property being chiefly determined by the degree of reaction and effective competition."	Shrubs in chaparral and desert ecosystems	Clements 1936:270
Ecological Engineer	"organisms that directly or indirectly modulate the availability of resources to other species, causing physical state changes in biotic or abiotic materials."	North American Beaver *Castor canadensis* (Naiman et al. 1986)	Jones et al. 1994:373
Foundation Species	"are disproportionately important to the continued maintenance of the existent community structure."	*Hedophyllum sessile, Strongylocentrotus purpuratus, Pycnopodia helianthoides*	Dayton 1972:86

Table 3. Competing terms close to keystone species in meaning.

crucial to the stability of the shoreline food web. The distinction between the two concepts thus appears to mostly reflect the notion that a keystone species has an influence in some way disproportionate to its abundance: a notion integral to most definitions of the keystone concept (Table 1), but one which appears hard to empirically test (above). In practice, a species may be both keystone and dominant, or it may in theory be one without quite being the other, assuming we can find a means to distinguish between proportionate and disproportionate degrees of influence and assuming that we can agree on whether the maintenance of stability is integral to one or both concepts.

A second area of overlap exists between keystone species and ecosystem engineers. Ecological engineers have been defined as "organisms that directly or indirectly modulate the availability of resources to other species, causing physical state changes in biotic or abiotic materials" (Jones et al. 1994:373). Examples include the North American Beaver (*Castor canadensis*), prairie dogs (*Cynomys* spp.) and the African Elephant (*Loxodonta africana*; Naiman 1988, Whicker & Detling 1988). As this list suggests, many species described as ecosystem engineers have also been described as keystone species, and it is unclear whether engineers have in fact been mislabelled as keystones. For example, while the Red-naped Sapsucker (*Sphyrapicus nuchalis*) has been described as a keystone species because of its habit of excavating nest holes that are used by a range of secondary cavity-nesting birds (Daily et al. 1993), this behaviour is better described as ecological engineering. It appears that misclassification may be a problem, a concern compounded by recent definitions of ecosystem engineers that have also introduced the idea that engineers provide ecological stability, much as keystones were originally argued to do (Dudgeon & Petraitis 2005). The overlap between the two concepts is also highlighted by the parallels between ecological engineers and 'keystone modifiers' (Lawton & Jones 1995). Keystone modifiers are defined as species which greatly affect habitat features without necessarily having direct trophic effects on other species (Mills et al. 1993). Caro (2010:144) argued that ecosystem engineers differ from keystone species in that they can act in concert, whereas keystones are always individual species, and because engineers alter their physical environments, whereas keystones influence their communities. While many supposed keystones are individual species, keystone mutualists act in concert in the same way ecosystem engineers are believed to act, and as outlined above, keystone modifiers can change their environment as well as their community. Caro (2010) did admit, however, that ecosystem engineers should be considered to be a subset of keystone species, and Power et al. (1996) argued that the two terms are interchangeable, therefore subsuming all engineers within the keystone concept.

An even more difficult distinction is between keystone and foundation species. Dayton's (1972) definition of foundation species (see Table 3) overlaps with both the dominant and keystone species concepts. Indeed the limited uptake of the term 'foundation species' in the literature suggests that it has been subsumed within the keystone concept, which is intriguing given that both Paine and Dayton were working in the same intertidal habitats in Mukkaw Bay at the same time, and yet had described them as separate concepts (Paine 1969, Dayton 1971, 1972).

Recent research has introduced more confusion. Ellison and colleagues defined a foundation species as one which "controls population and community dynamics and modulates ecosystem processes", and differentiated between foundation species and keystone species: keystones "…are usually top predators" and foundation species "usually occupy lower trophic levels" (Ellison et al. 2005:479). Furthermore, according to Ellison et al. (2005), the fifth class of Jones and colleagues' typology of ecological engineers, the 'autogenic ecosystem engineer' (Jones et al. 1994), is directly analogous to Dayton's (1972) foundation species. It is thus evident that there are a number of alternative ways in which the same community relationships can be defined, as well as a lack of clear separation between terms as they are used by different authors and in different sub-fields of ecology.

Conclusion

Although there are many more terms that overlap with the keystone concept, extricating all their exact definitions is beyond the scope of this paper. Indeed, figuring out the meaning of the keystone concept itself has turned out to be challenging enough. Although Paine may have originally meant for the keystone concept to be a metaphor (Paine 1995), it has been used as a scientific term for decades – despite the failed attempts to improve the precision and consistency of its use. Indeed, given the difficulties of providing a standard quantitative test to identify keystones, especially considering the context dependency of species' community importance and the practical problems with existing field methodologies, there appears to be little prospect of developing a robust definition with the required thresholds or criteria. We propose a definition that, if accepted, may provide a consistent reference point and simplify the confusion surrounding the term: 'a keystone species is a species that is of demonstrable importance for ecosystem function'. In the meantime, the list of species labelled as keystones will continue to grow. We see some danger in this because the agency the term has with policy makers and the public appears to owe more to the imagery of the keystone analogy than to scientific validation that particular species, guilds, or groups justify the use of the term in an objective sense. Perhaps, in the end, this is the real value of the term – not so much an operational scientific concept, but rather a metaphor, and one which allows scientists to convey swiftly and powerfully an image of the interdependency of living things, and of the potential for seemingly unimportant species to have, in practice, a really important functional role that merits conservation action (Barua 2011)?

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