

Keystone species: the concept and its relevance for conservation management in New Zealand

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ABSTRACT

The keystone species concept has proved both promising and elusive in theoretical and applied ecology. The term has its origins in Robert Paine's studies of rocky shore communities in California. When the top predator (a starfish) was removed the species assemblage collapsed, prompting the architectural analogy with the keystone of an arch. By definition keystone species are those whose effect is large, and disproportionately large relative to their abundance. They include organisms that (i) control potential dominants, (ii) provide critical resources, (iii) act as mutualists, and (iv) modify the environment. Identifying keystone species can be problematic. Approaches used include experimental manipulations, comparative studies, natural history observations, and 'natural experiments', but no robust methodologies have been developed. Our inability to monitor and manage all aspects of biodiversity has led to the development of paradigms that focus on either single-species (e.g. indicators, umbrellas or flagships) or whole ecosystems (ecological processes and habitats). Not surprisingly, both have their advocates and detractors. The keystone species concept, which retains a species focus while avoiding the need to examine every species, and emphasises processes that directly (e.g. predation, competition) rather than indirectly (e.g. nutrient cycling) control biodiversity, may allow managers to combine the best features of both these paradigms. By itself, however, the concept is unlikely to provide a panacea for biodiversity managers.

Keywords: Community importance index; context-dependent; functional role; organism controlling potential dominant; resource provider; mutualist; ecosystem engineer.

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1. Introduction

The 'keystone species' concept has proved both promising and elusive in theoretical and applied ecology. The term originates with Paine's work on a rocky shore community in California (Paine 1966). When he removed the top predator (a starfish, *Pisaster ochraceus*) from a section of the shore, the original 15-species assemblage was reduced to eight species. The collapse of a system as a result of the removal of one of its elements prompted the architectural analogy with the keystone of an arch. Subsequently, numerous species in a wide range of communities throughout the world have been claimed to have keystone status, often with little experimental or quantitative evidence. Power et al. (1996) dismiss many of these as 'anecdotal keystones'.

The idea that some species may function as keystones has not been without its critics (Mills et al. 1993; Hurlbert 1997), who argue that while the concept has 'developed tremendous currency and fashionability' it has also become increasingly ill-defined, and now means little more than 'important for something' (Hurlbert 1997). In defence of this position, opponents cite the vagueness of keystone definitions and their inconsistent usage in the literature, and an implied dichotomy between keystone and non-keystone species that has not been demonstrated in nature. As the causal metaphor it was originally intended to be (Paine 1995), Hurlbert concedes that the notion was 'appealing and harmless', but as a well-defined concept or phenomenon he concludes it 'has had a stultifying effect on ecological thought and argument'. But if keystone species do exist, and if they are widespread in nature, then the concept is clearly of value in understanding community function, and has important implications for managing ecosystems to maintain or enhance their biodiversity (de Maynadier & Hunter 1994; Simberloff 1998).

2. Keystone concepts

Of the various definitions of keystone species that have been attempted, perhaps the most useful is that given by Power et al. (1996) as 'a species whose effect is large, and disproportionately large relative to its abundance'. It is not enough for a species to be highly influential; its role must be great in relation to its relative biomass contribution. Beech trees in a beech forest are not considered keystones because their effect (while great) is not *disproportionate* to their relative abundance. In Power's terminology, such species are 'dominants'. In the architectural analogy, they might be considered 'foundation stone' species.

It is clear from the above definition that both aspects of keystones are a matter of degree. How great an effect is 'large'? How large a proportion is 'disproportionate'? Power et al. (1996) suggest using the 'community importance' (C.I.) index developed by Mills et al. (1993). This is the strength of the effect (or impact) of a species on a community (as measured by the change

in a community trait such as productivity, species richness, etc.) per unit change in a measure of the abundance (usually biomass) of the species. The effect may be positive or negative. The easiest way to determine the C.I. of a species is to remove the species entirely and measure the resulting change in a relevant community feature. A species with an impact proportional to its abundance would have a C.I. of 1. That of a keystone species would be greater than unity, though how much greater is still not defined (Power & Mills 1995; Power et al. 1996).

It seems probable that in any community the removal of individual species would reveal a spectrum of types from so-called 'redundant species' (whose removal has a negligible effect) to 'keystone species' (whose removal causes major changes). The existence of redundant species may be implicit in the concept of keystones because it suggests a hierarchy of species importance. However, the idea of a redundant species has been criticised conceptually and methodologically as a deficient paradigm. Gitay et al. (1996) point out the difficulty of defining, detecting or demonstrating redundancy. Navarrete & Menge (1996) show that previously 'redundant' species (whelks) with a low 'interaction strength' (the effect that one species exerts on another) can play a major role in a community if the former keystones (starfish) are removed. Both of the above papers argue strongly that, for conservation management purposes, no species should be assumed to be redundant.

An important point to emerge from several studies is that the keystone status of a species is entirely context-dependent. The community importance of the same species may vary from one ecological situation to another. Menge et al. (1994) demonstrated this in a series of experiments involving the original keystone species, the starfish *Pisaster ochraceus*. They showed that this species acts as a keystone by its predation of mussels (*Mytilus californianus*) on wave-exposed rocky headlands but not in sheltered areas nearby. Navarrete & Menge's (1996) experiments similarly showed that whelks (*Nucella* spp.) acted as keystones in the absence of starfish, but not in their presence. Even in apparently similar contexts, the keystone role can be adopted by different organisms. Fauth (1999) found that in comparable habitats in North and South Carolina the keystone role was adopted by different amphibians. In this sense 'keystoneness' is not an intrinsic property of a species, but of its functional role in a particular community assemblage. The diversity of organisms that have been shown to act as keystones indicates that they cannot be readily predicted on the basis of particular life-history traits. They can only be identified by examining their *function* in specific communities. For example, the prairie dog (*Cynomys ludovicianus*) has generally been considered a keystone species in North American grasslands, but this species inhabits a wide variety of grassland types. Stapp (1998) questions whether it necessarily plays a keystone role in all of them. Each grassland type is a different 'context' requiring a separate assessment of the prairie dog's role.

If the removal of a single species can cause major changes to the structure, function or diversity of a community, it follows that keystone-dependent communities are perhaps more vulnerable and potentially unstable than communities where keystones are absent. Power et al. (1996) point out that the extinction of species may result in a community becoming keystone-dependent. If several species share a trophic level, the removal of one of them may simply

result in compensatory action by the others as they expand in abundance or niche breadth. However, if all but one of the species in the group are eliminated (e.g. by human influence), the remaining species may come to play a keystone role it did not previously have. The avian fauna of New Zealand, for example, has been much depleted by human influence. It is possible that this may have placed some of the surviving species (e.g. kereru *Hemiphaga novaeseelandiae*) in keystone roles they did not formerly have, or at least increased their 'community importance'.

Another important way in which the ecological context can change markedly is by the *addition* of alien species. An added species could become a new keystone in a community where no equivalent or comparable species previously existed.

It has been suggested that rather than restricting the keystone concept to individual species, it should also be applied to groups of organisms (Willson & Halupka 1995) and major abiotic (e.g. frost, fire) processes (Bond 1994a). However, this dilutes the original concept to a point where all communities would have to be considered keystone-dependent. For example, every functional group (grazers, predators, pollinators, seed dispersers, detritivores) plays an essential role within its community, and the removal of even a subgroup would clearly be disruptive at some scale. Similarly, all communities are influenced by major abiotic processes. By contrast, a keystone is, by definition, a *single* object on which the forces holding an arch together are *concentrated*. Only cases where the responsibility for keeping a community intact (or dramatically altering it) resides in one species can be truly considered keystones.

3. Types of keystone species

The keystone role for a species can arise in several different ways. Here we distinguish four types of organism on the basis of their functional role as keystones: (i) organisms controlling potential dominants; (ii) resource providers; (iii) mutualists; and (iv) ecosystem engineers. These groups are not mutually exclusive, and individual keystone species may exhibit characteristics of more than one functional type.

3.1 ORGANISMS CONTROLLING POTENTIAL DOMINANTS

The classic keystone is an organism that controls the population of a potentially dominating species, thereby promoting coexistence by reducing competition amongst other species for a limiting resource. In the case of Paine's rocky shore community (Paine 1966; 1974), the primary resource is space, the potential dominant that tends to occupy all of the rock surface is the mussel (*Mytilus californianus*), and the keystone species that keeps the mussels in check is the starfish (*Pisaster ochraceus*). The removal of the mussels opens up enough rock surface to prevent competitive exclusion eliminating a range of less

competitive species. Another example of a top predator controlling species diversity in lower trophic levels is that of the triton gastropod *Charonia*, which eats the starfish *Acanthaster planci*, thereby preventing over-consumption of coral by the latter (Paine 1969). The removal of the triton results in loss of coral and consequent community degradation.

In terrestrial ecosystems, herbivores play a major role in maintaining the structure and species composition of the vegetation. The keystone status of many of them can be readily determined by removal experiments that follow the consequences for other elements of the community (e.g. Brown & Heske 1990). The effect of herbivores is often to suppress potentially dominant plant species, reducing competitive exclusion of less competitive species, and promoting a more species-diverse vegetation. Devries (1995) recognises the central role of large herbivores in the maintenance of many European vegetation types and advocates their use in large-scale nature reserves. However, large grazing herd-forming mammals might not qualify as keystones as their effects might not be considered disproportionate to their biomass contribution to the community. In contrast, the effect of some small herbivores may give them keystone status. Experimental removal of kangaroo rats (*Dipodomys* spp.) in the Chihuahuah Desert profoundly altered the whole community (Brown & Heske 1990; Heske et al. 1993; Kerley et al. 1997). Even very small herbivores can exert a very marked effect. Hanley et al. (1995) found that slugs and snails in grassland had a large influence on species composition and diversity because their selective grazing on seedlings resulted in differential recruitment. The biomass of vegetation eaten was negligible, but the qualitative effect of its removal was very marked, possibly giving the molluscs a keystone role in the community.

Grazers can act as keystones, but are often themselves top-down controlled by predators, which are then considered to have the keystone role. The recently reported case of sea otters (*Enhydra lutris*) on Adah Island, Alaska (Estes et al. 1998), provides an interesting example of the difficulties in deciding exactly which species in a trophic sequence is the keystone. Sea otters are part of the food chain: kelp forest, sea urchin (*Strongylocentrotus* spp.), sea otter, killer whale (*Orcinus orca*). The recent increase in predation by killer whales on the sea otters has resulted in a sharp decline in numbers of the latter species, leading to an 8-fold increase in sea urchins, and a 12-fold decline in kelp density. Loss of the kelp beds alters wave action and siltation rates with further effects on other inshore species, such as barnacles (*Balanus* spp.) (Kaiser 1998). This sequence of interactions has apparently been caused by killer whales shifting their diet to sea otters because of the decline in their normal prey of seals (e.g. *Phoca vitulina*) and sea lions (e.g. *Eumetopias jubatus*), itself due to the decline in fish stocks in the Bering Sea because of overfishing. In such a lengthy sequence of predators it is difficult to identify which species should be considered the keystone: one could as readily ascribe the role to the sea urchin, the sea otter, the killer whale, or the human (*Homo sapiens*). The removal of any one of these has a 'domino' effect on all the other organisms in the food chain.

This example illustrates the cascade principle first proposed by Darwin in the *Origin of Species* in which he notes that the activities of cats (*Felis catus*) could affect the population of red clover (*Trifolium pratense*). This was because cats eat field mice (*Apodemus sylvaticus*), which damage the nests of humble bees {bumble bees} (*Bombus* sp.) which, in turn, pollinate the clover flowers

(Darwin 1859, Ch.3). Keystone effects of this type are probably most frequent where relatively simple food chains exist without strong collateral connections that could absorb the removal of a particular link in the chain. Carpenter et al. (1985) show how trophic interactions cascade in a lake community. Strong (1992) suggests that cascades may be often aquatic with algae at the base; but that in complex food webs, consumption in any particular trophic level is so differentiated that the effect of removing any one species is normally buffered by its functionally equivalent colleagues. He argues that true trophic cascades imply keystone species, and that since all trophic interactions do not cascade, simple top-down control may not be the norm.

Disease-producing organisms can also function as keystones, where their impact on predator or herbivore populations has significant flow-on effects for dominant elements of the wider community. Some of the best-known examples are the rinderpest virus and the anthrax bacterium (*Bacillus anthracis*), which have periodically devastated grazing mammal populations in parts of eastern and southern Africa. Here the disease organism, by killing the herbivores and reducing the grazing pressure, facilitated a pulse of woody species regeneration and the displacement of extensive grassland communities by *Acacia* spp.-dominated woodlands (Prins & van der Jeugd 1993). Fungal pathogens may similarly fulfil a keystone role, most notably when introduced to communities dominated by non-resistant host species. Well-documented examples include chestnut blight (*Cryphonectria parasitica*), which has reduced the once-dominant American chestnut (*Castanea dentata*) to a minor understorey component in eastern United States forests (Anagnostakis 1995), and Dutch elm disease (*Ophiostoma ulmi* and *O. nova-ulmi*), which has similarly decimated American elm (*Ulmus americana*) populations (Karnosky 1979). In both cases the keystone role of the fungus is in removing a dominant canopy species, which can be expected to have significant flow-on effects for the rest of the forest community.

Keystone species have not been found in all communities where they have been sought. An attempt by Wright et al. (1994) to test the hypothesis that tropical forest regeneration was affected by the extinction of large carnivores through a cascade effect gave ambiguous results. Tanner et al. (1994) found that high species diversity in coral assemblages in the Great Barrier Reef was maintained, not by a single keystone species, but by the action of physical disturbance creating space for recruitment. One suspects that cases where keystones have been sought but not found are less likely to be published than cases that demonstrate their presence.

3.2 RESOURCE PROVIDERS

A second type of keystone species is one that provides a vital resource to a range of organisms at a time of scarcity (which often occurs seasonally). The resource provider itself may not be a particularly abundant species, but if it is removed, the dependent organisms are unable to bridge the gap in supplies. The most familiar examples involve the provision of keystone plant resources such as fruit during seasonal shortages (Terborgh 1986a; Van Schaik et al. 1993). Peres (1994) found that a small number of plant species provided a range

of resources in the dry season that acted as temporary alternative sources of nourishment for four primates in western Brazil. The resources included exudates, nectar, immature seeds as well as fruit.

Many tropical forest communities include numerous obligate frugivores, mainly birds, primates, bats and specialised insects. However, the availability of fruit varies markedly through the year, with each plant species exhibiting its own phenological pattern (Fenner 1998). 'Bottle necks' or 'pinch points' occur in the supply of fruit, and the few species of plant that fruit at those times provide a life-line that tides the frugivores over the period of dearth. Terborgh (1986b) estimates that in the floodplain forest of Cocha Cashu in Peru, only a dozen species of plants (out of trees, stranglers, vines and palms) in a total flora of 1000 species produce such keystone resources. In fact, it is possible that the presence of keystone fruit providers may determine the species diversity of the fruit-eaters. The Urucu terra firme forest in Brazil has a notably low density of frugivores in comparison with equivalent forests elsewhere. Peres (1994) suggests that this may be due to the severe periodic shortages of fruit that occur because of the strongly seasonal production of fruit in this community.

The fig genus (*Ficus*) stands out as being of central importance as a keystone resource provider in many tropical forests. One reason is the continuous aseasonal fruiting in this genus, which may be a consequence of the fig's reliance on specialised wasp pollinators (Milton 1991). In Malaysian lowland rainforests, at least 60 species of birds and 17 species of mammals eat figs. Lambert & Marshall (1991) show that a guild of 29 *Ficus* species in a Malaysian dipterocarp forest acted as keystone resource providers for a wide range of frugivores. However, in some forests, e.g. in the Western Ghats in India, *Ficus* trees are somewhat patchy in their distribution, and only act as keystone resource providers for highly mobile species with large home ranges. For less mobile animals, such as the Malabar giant squirrel (*Ratufa indica*), the figs acted as keystones only for those *individuals* whose home range included fig trees (Borges 1993). In other tropical forests, e.g. those in Gabon, figs are too scarce to act as lean-period keystone providers, and the role is filled by two species of Myristicaceae and one of Annonaceae for a range of monkeys and frugivorous birds (Gautier-Hion & Michaloud 1989).

Microbial organisms may also function as keystone resource providers where their presence enhances a limiting (usually nutritional) resource. On the island of Hawaii the invasive symbiotic nitrogen-fixer (*Myrica faya*) acts as a keystone resource provider in nitrogen-limited forest communities developing after vulcanism (Vitousek 1990). The increased nitrogen availability has flow-on effects for litter accumulation, earthworm populations (Aplet 1990) and nutrient cycling, causing major changes to the formerly open-canopied forests, including the displacement of dominant native tree species.

3.3 MUTUALISTS

Where two species are mutually dependent, the elimination of one will result in the demise of the other. In this sense they act as keystones for each other. What might be called 'group mutualisms' are common (e.g. between fruit producers

and seed-dispersing frugivores collectively, or between pollinators and groups of plants). But one-to-one codependency is a risky strategy and is probably rare in most communities. It is possibly more common in some types of organisms, such as orchids and their specialist pollinators. Darwin (1862) gives some remarkable examples of plant-pollinator co-evolution. Bond (1994b) describes cases of pollination mutualisms in the fynbos vegetation of the Cape, South Africa, where a number of plants are exclusively pollinated by a sparse fauna of long-tongued flies, oil-collecting beetles, monkey beetles, carpenter bees and butterflies. Certain birds in Malaysia are fig-eating specialists (Lambert & Marshall 1991), but the mutualism here is probably unequal as the fig does not depend exclusively on these specialist feeders for seed dispersal. More convincing cases of mutualists acting as true keystones arise where there is dependency of several species on a single mutualist. Manning & Goldblatt (1997) give an example of a guild of at least eight (unrelated) plant species with long tubular flowers, all of which depend exclusively on a single species of long-proboscid fly for pollination. Clearly, the insect here fulfils a keystone role.

Even a one-to-one mutualist could act in a keystone capacity if at least one of the partners had strong interactions with other species in the community. The removal of the mutualist pollinator of a dominant plant would markedly disrupt the community. Fig-wasps provide an interesting example of this. *Ficus* trees and fig-wasps are mutually dependent. The trees act both as major structural elements in the community and as keystone resource providers for frugivores. These frugivores are, in turn, essential seed dispersal agents for a wide range of *other* plants (Anstett 1997). The fig-wasp has an influence greatly disproportionate to its abundance, and is perhaps one of the most extreme examples of a keystone mutualist. The vulnerability of this mutualism is suggested by the recent work of Nason et al. (1998) showing that *Ficus* trees in the small Barro Colorado Island nature reserve, Panama, depend on cross-pollination from trees distributed over a wide area of the surrounding forest. The reserve is thus not self-contained for this keystone resource provider as it depends on forest management beyond its borders.

3.4 ECOSYSTEM ENGINEERS

Organisms can also act as keystones by modifying the physical environment in ways that release resources for other species. The activities of many organisms provide habitats that would not otherwise be available, often by means of disturbance to the physical habitat. Because of the structural alterations they bring about, such organisms have been referred to as ecosystem engineers (Jones et al. 1994). They can be considered keystone species if their effects are large and disproportionate to their abundance.

Examples of the action of ecosystem engineers are legion. They include dam building by beavers, which has major local effects on both terrestrial and aquatic habitats (Naiman et al. 1988); soil disturbance as a result of burrowing by a wide range of species such as rabbits, moles, badgers, prairie dogs, gophers and kangaroo rats; nest building by ants and termites; wallow creation by alligators,

vegetation destruction by elephants, and hole drilling by woodpeckers. The long-term engineering effects of earthworm action in soil have been known for over a century (Darwin 1881).

In most of these cases the provision of habitat or other resources is an incidental by-product of the engineer's activity. The benefiting organisms can be considered opportunists that have become adapted to exploit the resource. A good example of an 'incidental' provider of both habitat and food is the red-naped sapsucker (*Sphyrapicus nuchalis*) of the Colorado subalpine meadows (Daily et al. 1993). Its abandoned nesting holes in aspens are occupied by two species of swallow, whilst its feeding holes in willows provide sap flows for a range of birds, mammals and insects. Its engineering activities are thus quite modest, but the results are of disproportionate importance.

In some cases there is a high degree of adaptation in the benefiting species. Redford (1984) recorded the inquiline organisms (non-parasitic occupants) in termite mounds (of *Cornitermes cumulans*) in the Brazilian cerrado community. These included at least 17 other species of termite and ten species of ants (many of them obligate inquilines), as well as many other insects (beetles, flies, wasps and bees) and other invertebrates (scorpions, centipedes, spiders) and vertebrates (lizards, snakes, mice and birds). Termites are true ecosystem engineers and can be considered to have a keystone status in this region as their elimination would have a major effect on community structure and species diversity.

In assessing the keystone role of an organism it is not always possible to distinguish clearly between the effects of predation and engineering. A good case can be made for considering large grazers as keystone ecosystem engineers, as well as herbivores. By suppressing invasion of woody species and maintaining open grassland vegetation they profoundly alter the physical structure of the community. Even the classic keystone predator, the starfish *Pisaster*, exerts its influence not just as a predator but as the incidental creator of bare patches, which provide recruitment sites for other species. Most organisms probably alter their environment in some way that can be exploited by other species. Whether the engineer can be considered a keystone species is a matter of degree: how profound the physical effect is, how disproportionate it is, how many other species benefit, and how great their dependence on the alteration is.

4. The New Zealand context

In the late 1960s Paine visited New Zealand and repeated his original predator removal experiment (Paine 1966) on the rocky intertidal communities at Anawhata, just north of Piha, near Auckland (Paine 1971; Paine et al. 1985). During the 9-month period that the top carnivore (a starfish, *Stichaster australis*) was removed from the experimental plots, the area occupied by its primary prey (the green-lipped mussel, *Perna canaliculus*) almost trebled, the mussel expanded its intertidal range, and the species assemblage of the experimental plots reduced from 20 to 14. Since that time there have been few references to keystone species, or studies of their functional importance, in the New Zealand ecological literature. There are, however, numerous examples of organisms that may fulfil a keystone role in our natural ecosystems.

4.1 ORGANISMS CONTROLLING POTENTIAL DOMINANTS

The decline of much of the native fauna has been linked to introduced predators such as feral cats, rats (including kiore) and stoats (Holdaway 1999; Innes et al. 1999; Lloyd & Powlesland 1994). However, for the predators to be considered keystones the removal of the prey species needs to affect dominant components of the ecosystem, and to date few such links have been clearly demonstrated. In freshwater ecosystems, exotic fish species such as brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) are credited with the decline of native fish (*Galaxias* spp. and *Gobiomorphus* spp.), crayfish (*Paraneohrops* spp.) and insect populations (Cadwallader 1975; McDowall 1968, 1987; Townsend & Crowl 1991), and may be a factor in the decline of the blue duck (*Hymenolaimus malacorhynchos*) (Towers 1996). Trout species may warrant keystone status where their presence has a disproportionate effect on the abundance or biomass of the freshwater biota. However, because the impact of adjoining land use tends to dominate stream ecology, demonstrating a keystone role for trout may not be a straightforward process.

The keystone role of introduced herbivore species is more readily demonstrated. On Stewart Island, where coastal forests are periodically subject to salt-spray-related dieback, white-tailed deer (*Odocoileus virginianus*), by preventing the regeneration of the canopy tree species, play a keystone role in the replacement of these forests by shrubland, fernland or grassland communities (Stewart & Burrows 1989). A similar situation occurs after fire in podocarp-tawa (*Beilschmiedia tawa*) forests in the northern Urewera ranges (Payton et al. 1984). Where previously, dense pole stands of kanuka (*Kunzea ericoides*) acted as a nurse crop, initially for kamahi (*Weinmannia racemosa*) and later for the podocarp/hardwood species characteristic of the pre-fire forests, deer now prevent kamahi regeneration and maintain the dominance of the early successional kanuka tree species. Australian brushtail possums (*Trichosurus vulpecula*), by defoliating and killing canopy trees, can also be considered to play a keystone role in many New Zealand forests. Where the dominant tree

species are preferred foods, possum browsing may lead to the collapse of forest canopies over large areas (Batcheler 1983; Rose et al. 1992), and their replacement by forest or shrubland communities less palatable to the ungulate browsers. In both cases the keystone role of the herbivore results from the large and disproportionate influence it has on the dominant elements of the forest community, which is exacerbated by the absence (except for humans) of top-down predator control. In the short term (< 150 years since the introduction of mammalian herbivores) the keystone function of the ground browsers is most evident where forests are regenerating after disturbance, but over the lifetime of the forest both ground and arboreal browsers can be expected to have an overriding influence on the composition and structure of the vegetation.

Vertebrate herbivory does not invariably result in the removal of native dominants. In some communities rabbit (*Oryctolagus cuniculus*) and sheep (*Ovis aries*) grazing fulfils a positive keystone role by preventing dominant native plant species being overtaken by more aggressive adventive grasses and other weeds. The cessation of sheep grazing significantly reduced the number of both indigenous and adventive plant species, and increased the dominance of adventive grasses such as cocksfoot (*Dactylis glomerata*) in highly modified silver tussock (*Poa cita*) grasslands on the Port Hills near Christchurch (Lord 1990). On Motunau Island off the north Canterbury coast, the removal of rabbits (Cox et al. 1967) resulted in much of the silver tussock grassland that formerly dominated the island being replaced by adventive shrubs, forbs and grasses (I. Payton, pers. obs.), which were previously suppressed by the rabbits. Similarly, exclusion of sheep from Danthonia (*Rytidosperma* spp.) grassland reserves on the Canterbury Plains has allowed the browse-tolerant native grasses to be displaced by more aggressive adventive grasses (Meurk et al. 1989). In each case the selective grazing pressure of the keystone herbivore is required to maintain the indigenous character and/or the diversity of the grasslands.

Rabbit haemorrhagic disease (RHD), which was illegally introduced into New Zealand in August 1997, may also have a keystone role in at least some grassland ecosystems. In addition to changes to vegetation composition resulting from fewer rabbits and reduced levels of herbivory (Norbury & Norbury 1996), prey switching by rabbit predators is expected to adversely affect native grassland fauna, at least in the short term (Norbury 1999). The likely keystone role for the virus results from its ability to initiate disproportionately large changes in plant and animal biomass and diversity within the grassland, relative to its own abundance. The recently isolated disease organism '*Phytoplasma australiense*', which causes flax yellow leaf, cabbage tree sudden decline (Andersen et al. 1998a, b) and coprosma lethal decline (R. Beever, pers. comm.) may also warrant keystone status, at least in plant communities where the affected plant species predominate.

The keystone status of each of these organisms is clearly context-dependent. Although the possum may function as a keystone species in rata-kamahi forests, the same cannot be said for its role in beech-dominated ecosystems where floristic composition but not forest structure is typically affected (Wardle 1984). Rabbit haemorrhagic disease has significantly reduced rabbit populations in many semi-arid grassland communities, but has thus far had little effect in areas of higher rainfall and would not be expected to play a keystone role in these ecosystems.

Likewise the cabbage tree sudden decline epidemic, which began in the early 1980s, has resulted in the loss of large numbers of cabbage trees in the northern half of the North Island, but has had little or no effect on South Island cabbage tree populations (Beever et al. 1996).

Invasive plant species are also potential keystones where they displace dominant elements and substantially alter the species composition of existing communities. In remnant and disturbed forest stands Old Man's Beard (*Clematis vitalba*) vines alter forest structures by smothering mature trees (Williams & Timmins 1990; West 1992) and, together with the adventive herb Wandering Willie (*Tradescantia fluminensis*), affect plant species composition by inhibiting seedling regeneration (Kelly & Skipworth 1984). On alluvial sites the naturalised shrub buddleia (*Buddleja davidii*) rapidly displaces primary native colonisers, and can accelerate successions to mature forest by replacing longer-lived natives such as kanuka (Smale 1990). Adventive hawkweed (*Hieracium*) species play a similar role in many grassland communities, displacing the dominant tussocks (Makepeace 1985) and reducing indigenous species diversity (Rose et al. 1995).

In freshwater ecosystems such as Lake Taupo, the adventive macrophyte *Lagarosiphon major* has significantly altered plant species composition and biomass over large areas of the littoral zone. In addition to directly displacing the native plant species, *Lagarosiphon* acts as a keystone resource provider for adventive black swan (*Cygnus atratus*) populations (Bull 1983) whose grazing activities also uproot native macrophyte (e.g. *Potamogeton* spp.) communities (Howard-Williams & Davies 1988). Increased detritus resulting from the grazing activities of the swans provides an added food source for native koura (freshwater crayfish, *Paranephrops planifrons*) populations, which in their turn influence species richness and invertebrate biomass (Parkyn et al. 1997), and limit the depth to which native macrophyte communities extend (Coffey & Clayton 1988).

4.2 RESOURCE PROVIDERS

Organisms that may act as keystone resource providers can be found at a range of trophic levels in New Zealand ecosystems. The low levels of nitrogen and phosphorus in many New Zealand soils provide a potential keystone role for nitrogen-fixing organisms and mycorrhizal fungi. Nitrogen-fixing bacteria are known from native plant genera such as *Carmichaelia*, *Coriaria*, *Discaria*, and *Sophora* (Greenwood 1978; Torrey 1978) that are, typically, early colonisers of disturbed sites, and are the basis for legume introductions to enhance grassland productivity (Sears 1960) and assist the establishment of exotic pine plantations on sandy soils (Gadgil 1971). Where phosphorus is the nutrient limiting plant growth, native mycorrhizal fungi have been shown to be essential for the growth and survival of a wide range of native tree and shrub species. Conversely, the lack of suitable mycorrhizal fungi has been used to explain the slow spread of beech (*Nothofagus*) species into adjacent plant communities (Baylis 1980). In both cases the possible keystone role for the resource provider results from changes to plant community composition initiated by the increased nutrient availability. Both examples can also be viewed as keystone organisms

controlling potential dominants and, where the micro-organism: host plant relationship is close and/or obligate, as keystone mutualists.

For island ecosystems Daugherty et al. (1990) have suggested a keystone role for seabird populations whose guano, by enriching soil fertility, supports high densities and diversities of invertebrates and reptiles. However, closer examination of the influence of seabirds and rats in island ecosystems (Markwell 1999) has concluded that although both groups have important roles on offshore islands, neither conforms to the definition of a keystone species.

Amongst the native invertebrates perhaps the clearest example of a keystone resource provider are the beech scale insects, *Ultracoelostoma* spp., which secrete a sugary exudate known as honeydew (Morales et al. 1988). In beech forests where these insects are common, honeydew is an important food source for nectar-feeding birds such as tui (*Prosthemadera novaeseelandiae*), bellbird (*Anthornis melanura*) and silvereye (*Zosterops lateralis*) (Gaze & Clout 1983), particularly in the winter (Wardle 1984). Over recent decades the availability of this abundant high-energy food supply has allowed two invading species of *Vespula* wasps to reach high densities in honeydew beech forests (Thomas et al. 1990). In addition to directly affecting the nectar-feeding birds, wasp predation has depleted invertebrate populations (Beggs & Rees 1999) which, in turn, has adverse effects for insectivorous bird populations in these forests (Moller & Tilley 1989; Moller et al. 1993). The keystone role for the scale insect results both from the direct provision of a vital food source at times of scarcity, and from the indirect consequences of this resource for other groups of organisms within the beech forest ecosystem.

Obligate frugivores are uncommon in the New Zealand avifauna and elsewhere. While a relatively high proportion of New Zealand's native plants (c. 250 species) have fleshy fruits, fewer than 12 native bird species are regular frugivores and only the endemic flightless parrot kakapo (*Strigops habroptilus*) is thought to be dependent on periodic heavy (mast) fruiting years for breeding success. Availability of fruit varies markedly between plant communities (e.g. podocarp-hardwood forests > beech forests), seasons (late summer → late winter > early spring → summer) and years (Clout & Hay 1989; Lee et al. 1990). Fleshy-fruited species that may fulfil a keystone role for native frugivores fall into three categories, (i) those that enable the build-up of energy reserves before winter (e.g. kereru consumption of tawa and miro (*Prumnopitys ferruginea*) berries—McEwan 1978), (ii) those that provide a reliable source of fruit during periods when alternative foods are scarce (e.g. supplejack *Ripogonum scandens*), and (iii) those where periodic heavy (mast) fruiting is associated with successful breeding (e.g. kakapo consumption of pink pine *Halocarpis biformis* seed—Powlesland et al. 1992).

For the takahe (*Porphyrio mantelli*), a flightless endemic rail now restricted to the Murchison Mountains in Fiordland, rhizomes of the summer-green fern *Hypolepis millefolium* provide a critical energy source during winter when snow forces birds from their summer grassland range (Mills et al. 1980). Similarly, high levels of available carbohydrate in fern (*Blechnum* spp.) and clubmoss (*Lycopodium ramulosum*) rhizomes provide a reliable source of energy for the kakapo (James et al. 1991). In both cases the possible keystone role of the plants is the provision of an essential resource in an environment and at a time of the year when alternative sources are scarce.

4.3 MUTUALISTS

Specialist pollinators are not a feature of the New Zealand flora (Lloyd 1985), and there are few documented examples of one-to-one codependency (Webb & Kelly 1993). The recently described cases of bat pollination of the root parasite *Dactylanthus* (Ecroyd 1996), and honeyeater pollination of mistletoe flowers (Ladley & Kelly 1995; Ladley et al. 1997) may warrant consideration as potential keystone relationships. Video camera surveillance of *Dactylanthus* flowers suggests this species is pollinated almost exclusively by an endangered endemic bat (*Mystacina tuberculata*), but that in the absence of the bats the introduced ship rat (*Rattus rattus*) can assume this role. For the *Peraxilla* mistletoes, pollination is dependent on two species of endemic honeyeater (tui and bellbird), which twist the top of the ripe buds and trigger an explosive opening mechanism. Flowers not visited by birds fail to open and only a minority set seed. In both cases seed production and hence the long-term survival of the plant species is heavily, but not entirely, dependent on a single pollinator or pollinator-group. In neither case is the affected plant species either a dominant member of its community or a demonstrated part of a wider trophic cascade affecting dominant elements of a community.

The decline or extinction of much of the native terrestrial avifauna raises questions about their role as seed dispersers in pre-human times, whether guilds of native seed dispersers may now be absent or reduced to single (perhaps keystone) species, and the extent to which introduced species now fill these roles. Among the extinct avifauna, moas (Dinornithiformes), huia (*Heteralocha acutirostris*) and piopio (*Turnagra capensis*) ate fruit or seeds of a wide range of tree and shrub species (Burrows 1989; Clout & Hay 1989), but their demise has not resulted in the obvious regeneration failure of any native plant species (Lee et al. 1990). Of the extant frugivores, Clout & Hay (1989) consider kereru the most important seed disperser in New Zealand forests because of its catholic diet (≥ 70 plant species), mobility, and widespread distribution. The kereru may also warrant keystone status as the sole surviving disperser of larger (>10–12 mm) seeded native tree species (Lee et al. 1990); although Webb & Kelly (1993) consider this may overstate the importance and effectiveness of seed dispersal by birds. For the native loranthaceous mistletoes, where germination is entirely dependent on bird dispersal to remove the exocarp, Ladley & Kelly (1996) conclude that while the current size of native frugivore (bellbird, silvereye, tui) populations does not appear to threaten mistletoe survival, the [keystone] role of the dispersers needs to be considered when assessing historical or future mistletoe declines. Reductions in native frugivore populations have been partly offset by introduced European frugivores such as the blackbird (*Turdus merula*) and song thrush (*T. philomelos*) (Clout & Hay 1989). In addition to dispersing many of the same fruits as their native counterparts, the introduced frugivores target a wider variety of adventive weed species, and may play a keystone role in the changing composition of secondary shrub and forest communities (Burrows 1994; Williams & Karl 1996). The extent to which introduced brushtail possums, which also consume a wide variety of fruits (Cowan 1990), may fill the seed dispersal role formerly held by native avian frugivores may also be worth considering.

The possibility that at least some native lizards act as keystone mutualists also warrants examination. Geckos (*Hoplodactylus* spp.) and skinks (*Oligosoma* and *Cyclodina* spp.) include considerable quantities of fruit in their diets, and while foraging distances are small (cf. frugivorous birds) this may be partially offset by the longer time that seeds take to pass through the gut (Whitaker 1987). If keystone mutualist relationships involving lizards exist, they are most likely to be found among divaricate shrubs such as *Melicactus alpinus*, where fruits are inaccessible to many birds. Historically, the now extinct *Hoplodactylus delcourti* (the largest known gecko) may also have played a [keystone] role in the dispersal of large fruits (Webb & Kelly 1993).

4.4 ECOSYSTEM ENGINEERS

As with other keystone categories, some of the clearest New Zealand examples of ecosystem engineers are found amongst introduced plant and animal species. Until recent decades, introduced herbivores such as deer (e.g. *Cervus* spp.), goats (*Capra hircus*), chamois (*Rupicapra rupicapra*) and thar (*Hemitragus jemlabicus*) were seen as the primary cause of accelerated high-country erosion (Holloway 1959). While natural erosion associated with geological instability is now known to be more widespread than previously thought (Mosley 1978; Grant 1989; McSaveney & Whitehouse 1989), there can be little doubt that the impact of wild animal populations on understorey and litter layers has lessened the ability of native forest and grassland communities to absorb and retain moisture, and has altered hydrological regimes and biogeochemical cycles.

Adventive plant species also modify catchment hydrology. Willows (*Salix* spp.) used to stabilise riverbanks and estuarine plantings of cord grass (*Spartina* spp.) trap sediment, reduce the capacity of rivers, estuaries and wetlands to accommodate flood events (Partridge 1987; Russell 1994), and threaten biological diversity (Lee & Partridge 1983; Collier 1994). Replacement of native (*Chionochloa*) grasslands with plantation (mainly *Pinus* spp.) forests reduces both the magnitude of flood events and stream flows during periods of low rainfall (Fahey & Jackson 1997) which, in turn, affects aquatic flora and fauna and downstream ecosystems. The deeper-rooted conifers also increase nutrient availability in the topsoil (Davis & Lang 1991), which can be expected to provide a competitive advantage for adventive forbs and grasses with higher nutrient requirements than their native counterparts. In the braided river systems of the eastern South Island the spread of willows and Russell lupins (*Lupinus polyphyllus*) has resulted in the channelling of formerly meandering streams, a loss of open riverbed habitat for several rare or endangered birds (e.g. black stilt *Himantopus novaezelandiae*, wrybill plover *Anarchynchus frontalis*), and increased cover for their predators (Hughes & Warren 1997; Maloney et al. 1999).

Other adventive plant species that may function as ecosystem engineers include marram grass (*Ammophila arenaria*), gorse (*Ulex europaeus*) and *Hakea* spp. Marram, whose roots and stems are more effective sand binders than the native pingao (*Desmoschoenus spiralis*), changes the morphology and disturbance regimes in sand dune systems (Esler 1978). Gorse and *Hakea* spp., which have

high rates of litter production and accumulation, have the potential to alter fire regimes (Druce 1957; Fugler 1982) and affect the biota over large areas.

Amongst the introduced fauna, rabbits, whose burrows endanger seabird (Cox et al. 1967) and sealion (*Phocarctos bookeri*) (Crawley 1990) populations, feral pigs (*Sus scrofa*), whose rooting habits provide ideal establishment sites for beech seedlings (Wardle 1984), and European or koi carp (*Cyprinus carpio*), which cause significant damage to freshwater ecosystems by undermining stream banks (McDowall 1990), may warrant consideration as ecosystem engineers.

5. Identifying keystone species

Identifying keystone species is problematic (Power et al. 1996), and attempts to develop a set of species traits that would *a priori* determine keystone interactions have thus far proved elusive (Menge et al. 1994). A variety of approaches have been used, either singly or in combination, including experimental manipulations, comparative studies, natural history observations, and 'natural experiments' (Power et al. 1996), but no robust methodologies have been developed.

Experimental removal is the most convincing way of demonstrating the [keystone] role of an individual species in a particular community, but is frequently impractical for logistical, technical, social, or ethical reasons. To avoid the need for numerous manipulations to determine the presence and identity of the keystone species in a community, Power et al. (1996) suggest combining manipulative experiments with modelling approaches such as path analysis (Wootton 1994). Using this approach, one or a few strongly interacting species are experimentally reduced or removed, and the response to these changes is monitored in a much wider range of species within the community. Interpretation of removals is not always straightforward. Where experimental treatments (e.g. exclosure fences) remove more than one species (e.g. rabbits and sheep), it is often not possible to determine whether changes to the unmanipulated state result from the actions of a single keystone species, or the collective impacts of several members of a guild or trophic level (Power et al. 1996).

The time required to determine the consequences of experimental manipulations for other species in the community and the spatial scales over which the results are applicable are both extremely variable (Power et al. 1996). As a general rule, the impact of species manipulations occurs more rapidly in aquatic ecosystems (Estes 1995). For example, while Paine (1971, 1974) was able to demonstrate significant changes resulting from the removal of starfish from rocky shore communities within less than 12 months, the full effects of removing top predators from forest ecosystems may not become apparent for decades or even centuries (Dirzo & Miranda 1990; Terborgh 1986b).

The use of natural history observations, or comparative studies which substitute space for time (i.e. use habitats with varying densities of putative keystone species), overcomes many of the limitations of experimental manipulations. By themselves both approaches lack the rigour of experiments, the former because

of its subjective nature and the latter because no two sites are ever exactly the same. However, when used in conjunction with experimental manipulations, both can be extremely useful for identifying hypotheses and determining the generality of experimental results (Paine 1995; Power et al. 1996).

Large-scale changes in species abundance resulting from the invasion of organisms into new environments, the overharvesting of natural populations, or the deliberate eradication of pest species also offer opportunities for determining the potential keystone role of species. The use of such 'natural experiments' overcomes many of the social and ethical problems associated with deliberate experimental manipulations. Problems frequently associated with this approach include the lack of a pretreatment baseline, an inability to find comparable non-manipulated sites, and the replication of treatments (Carpenter 1989).

6. Implications for conservation management

Conservation managers are faced with a bewildering array of species, communities and ecosystems, each subject to a variety of internal (e.g. successional) and external (e.g. pest and weed) influences, which impose continual change at all levels. Faced with this complexity and ever-increasing demands for limited resources, the question still remains: what is the best way to maintain indigenous biodiversity and retain functional natural ecosystems?

The inability to monitor and manage all aspects of biodiversity has led to the development of paradigms that focus on either single-species (e.g. indicators, umbrellas or flagships) or whole ecosystems (Tracy & Brussard 1994; Simberloff 1998). Not surprisingly, each have their advocates and detractors. Among the single-species approaches, indicators create disagreement over what they indicate (Landres et al. 1988), umbrellas (species requiring large areas of natural habitat for their continued survival) raise questions over the range of biological diversity they shelter (Franklin 1994), and flagships (iconic species) are often notoriously expensive to keep afloat (Shrader-Frechette & McCoy 1993) and may require management regimes that clash with other elements of the natural biota (Ehrlich et al. 1992).

In contrast, ecosystem or landscape-scale paradigms emphasise ecological processes (e.g. nutrient cycling) and habitats rather than individual species (Franklin 1993; Meffe & Carroll 1994), using the rationale that biological diversity is best preserved by maintaining healthy ecosystems (Bourgeron & Jensen 1993). To do otherwise, proponents argue, will exhaust our available time and financial resources, society's patience, and scientific knowledge, long before we make significant progress towards the preservation of existing biodiversity (Franklin 1993). Opponents contend that where processes become the focus of biodiversity management, the process rather than the species it supports becomes what is valued. Because most ecosystem processes are

common to many species, the disappearance of threatened species may cause little or no detectable change to any key process. Further, they argue that whereas species are readily defined, ecosystems are arbitrary constructions that can range from individual water droplets to the entire biosphere (Tracy & Brussard 1994). The use of adaptive management regimes (i.e. ongoing modification of management practices based on observations of their outcomes) to implement ecosystem-based approaches also comes in for criticism on the basis that while they may provide 'rules-of-thumb' for managers, they tell us little about the mechanisms that maintain species, communities or ecosystems (Simberloff 1998).

In a paper that discusses options for managing biodiversity, Simberloff (1998) suggests that the keystone species concept may allow conservation managers to combine the best features of single-species and ecosystem-based management approaches. He argues that the use of keystones retains a species focus while avoiding the need to examine every species, and emphasises the mechanisms that directly (e.g. predation, competition) rather than indirectly (e.g. nutrient cycling) control biodiversity. Where it is possible to identify a keystone that is critical for the continued survival (or demise) of many other species in its community, management of that keystone may be an efficient means of managing a much wider range of biodiversity.

By themselves, keystone species are unlikely to provide a panacea for biodiversity managers. Not all (natural) ecosystems of interest may contain keystone species, and even where keystones are identified they may not be easily managed as part of a conservation strategy. However, even if this worst-case scenario eventuates, the search will have provided us with much useful information on the structure and functioning of ecosystems that will assist our attempts to conserve biodiversity.

To date there have been few detailed studies of keystone species, and almost none relating to New Zealand ecosystems. The challenge for New Zealand researchers, whether or not they embrace the keystone species concept, is to determine the interactions and functional significance of individual [keystone] species and guilds within our natural ecosystems. This approach will allow us to identify a hierarchy of importance amongst cohabiting species, and can be expected to produce critical information for conservation efforts to preserve indigenous biodiversity.

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