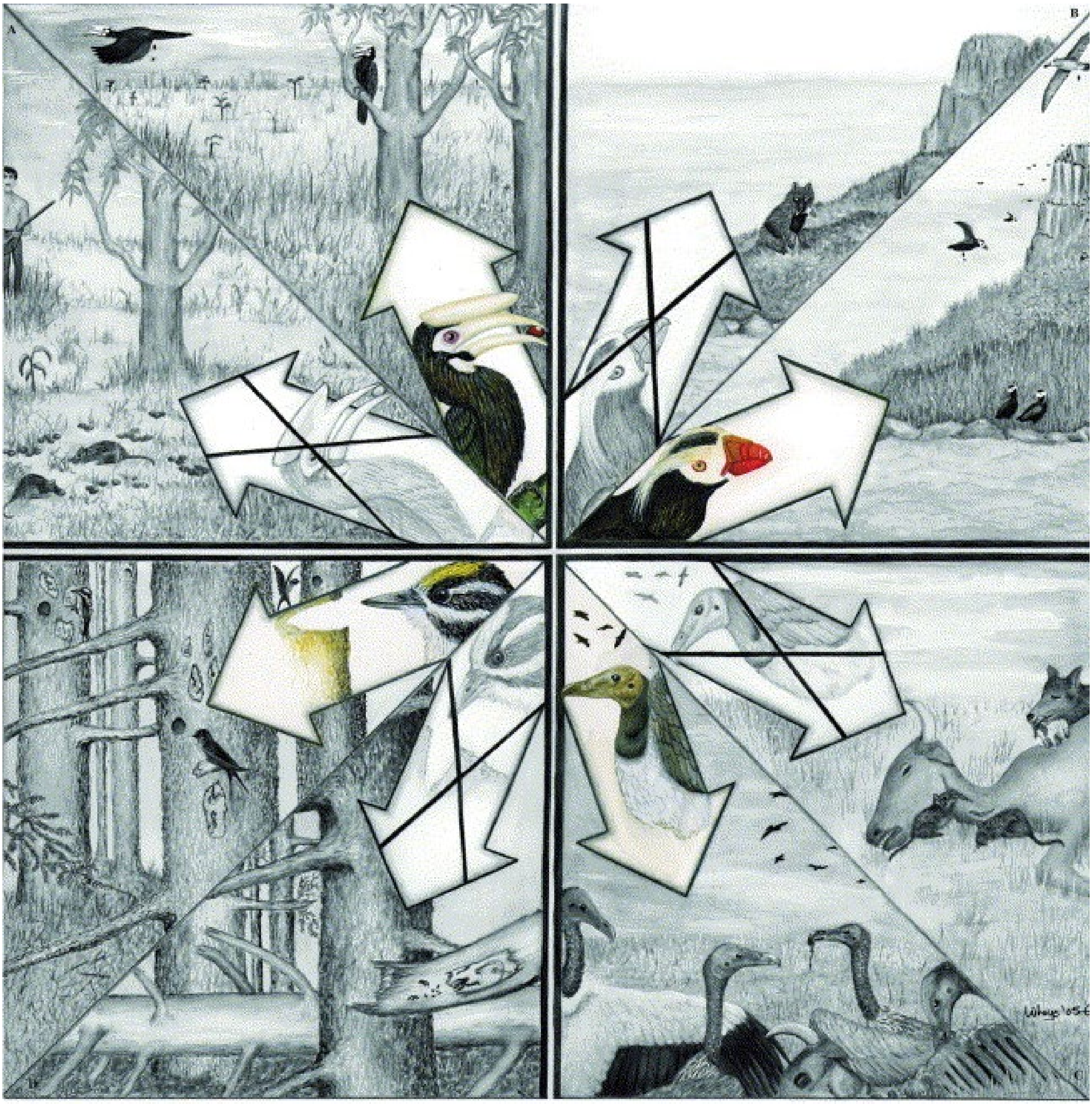
Ecosystem consequences of reintroducing keystone bird species



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Abstract

The increased need for biodiversity conservation, due to the critical situation of biodiversity, has created demand for efficient methods to focus conservation efforts. One of such methods that has come to the foreground of conservation biology is the keystone species concept. This concept indicates the exceptional importance of a species for the functioning of ecosystems and allows improved focus of preservation methods. Mammals seem overrepresented in studies of the keystone species concept and only few studies investigate birds as keystone species. To discover if the underrepresentation of birds, implying that they are not as relevant as keystone species as mammals, is justified, I performed an investigation into the significance of birds within three specific categories of ecological roles within ecosystems. I present an overview of avian predators, ecosystem engineers and scavengers performing similar roles as their mammalian counterparts. When populations of these species increase or decrease, cascading effects are visible. This indicates that these bird species are keystone species. This suggests that the scarcity of studies of birds as keystone species is due to a taxonomic bias in research and not because of birds being less relevant as keystone species. With this literature review, I show that bird species do perform keystone functions within various ecosystems in ways equal to mammals.

Introduction

Reintroducing species into their original ranges has developed into a key tool of conservation only recently (Seddon et al., 2007). Before the late 1990's, reintroduction was scarcely used as a form of biodiversity management, but more frequently as a tool of area management and pest control (Carvalho et al., 1998; Antkowiak & Hayes, 2004; IUCN/SSC, 2013). Ever since the extinction of species has gained more attention as a serious issue in preserving ecosystems and their important functions, reintroduction gained in popularity and is now a fully-fledged method in biodiversity conservation (Kleiman, 1989; Ceballos et al., 2015).

An important concept that is often used in combination with reintroduction is the keystone species concept. This concept was coined by Robert Paine in 1969 when he described the structural processes of intertidal habitats (Paine, 1969). This concept is used to define species that perform such a role in an ecosystem that without this specific species the ecosystem would collapse, as if an arch would collapse without the keystone. Throughout the years, the keystone species concept has had many applications and discussion has arisen as to what the definition should specifically be (Mills et al., 1993). Mills et al. (1993) state that a keystone species has two features that are essential to the concept: "First, their presence is crucial in maintaining the organization and diversity of their ecological communities. Second, it is implicit that these species are exceptional, relative to the rest of the community, in their importance." Throughout the years, many definitions have been proposed, e.g. Davic (2003) who redefined the concept to: "A keystone species is held to be a strongly interacting species whose top-down effect on species diversity and competition is large relative to its biomass dominance within a functional group." These different definitions demonstrate that the keystone species concept is an ever-evolving concept and might be an essentially contested concept, so one conclusive definition might never be found (Gallie, 1956). In this paper, I will apply the concept in the way stated by Mills et al. (1993), which is the most flexible definition and allows for a broad view on ecosystems, ecological communities, and/or food webs. Perhaps the best-known example of a keystone species is the classic predator that keeps prey species abundance in check so these prey species do not overexploit their food resources which would cause the ecosystem or food web to collapse (Paine, 1966). However, many more applications of 'keystone' on species are known (Figure 1, see Appendix A).

The keystone species concept is relevant for conservation as conservation efforts are often limited in resources and to increase the efficiency of these efforts keystone species have received much attention (Carroll, 1992). The argument for specifically targeting keystone species in conservation projects is that the protection of keystone species has beneficial effects for the entire ecosystem or prevents major damage to this ecosystem. The ecosystem consequences of the extinction of a keystone species are so severe that conservationists often try to prevent such events at all costs. These consequences vary from the overcrowding by prey species when a predator is removed from the system to the extinction of habitat engineers causing a cascade of secondary extinctions (Estes & Palmisano, 1974; Duggins, 1980; Riechert & Bishop, 1990; Christianou & Ebenman, 2005; Borrvall & Ebenman, 2006; Dunne & Williams, 2009). The reintroduction of keystone species seeks to achieve an opposite effect; a positive cascading effect. Predators in an ecosystem exert pressure unto herbivores and they adapt their behaviour accordingly, which leads to a specific browsing pattern and thus this influence of predators has its effect throughout the entire food web; a cascading effect. For example, reintroduced grey wolves (*Canis lupus*) prevent overpopulation of their prey species and in this way avert overeating of flora. This allows secondary herbivores to thrive and ultimately leads to higher biodiversity (Lavallée, 2018). An example of a species that would cause a cascade of secondary extinctions when removed is the banner-tailed kangaroo rat (*Dipodomys spectabilis*). Kangaroo rats dig burrows and leave nutrient-rich faeces at the entrance of these burrows. Certain plants are only able to grow on these enriched burrow-mounds, so when the kangaroo rats disappear, so would these plant species eventually (Krogh et al., 2002).

Most examples of such cascading effects in ecosystems come from studies involving large mammals, where animals and their interactions are more clearly visible and easily studied. There is currently a strong taxonomic bias in studies involving the keystone species concept, where mammals are over-represented even though many other taxa seem crucial in the health of many ecological communities

(Hale & Koprowski, 2018). Especially bird species have been neglected when the keystone species concept is involved (Hale & Koprowski, 2018), which is surprising as birds are known to perform important roles within ecosystems (Whelan et al., 2008).

The goal of this paper is to investigate if and how the reintroduction of bird species causes cascading effects in ecosystems and to examine if the scarcity of studies on birds is an effect of bird species being less important participants in ecological communities or if there is just a bias in research focus. I will give an overview of the current knowledge of bird species as keystones within ecosystems. To do this, I will review reintroductions of species in three broad categories, namely predators, ecosystem engineers and scavengers. Globally, these three categories form important functions within ecosystems that are often viewed as keystone functions. Predators not only keep populations of prey species in check, but are also known to create a landscape of fear, thus having a great influence on the foraging behaviour of prey species (Laundré et al., 2001). Sequentially, this causes an altered pressure on flora which will transform the overall habitat. Like predators, ecosystem engineers also transform their habitat, but not through a secondary effect. Species in this category take matters into their own ‘wings’, by adjusting the ecosystem to their preferences. They change the habitat they occur in through actions like cavity creation by woodpeckers or through caching of seeds by crows and jays. Scavengers also create opportunities for other species, like ecosystem engineers, by enabling access to nutrients otherwise inaccessible. However, scavengers do not engineer or create, but act upon biotic factors, by finding and opening up a cadaver. Scavengers are critical in enabling nutrients to reach other trophic levels (Buechley & Şekercioğlu, 2016).

I will briefly discuss conservation of keystone species itself and its hardships. Even if a (locally) extinct species is deemed to be a keystone to its former environment, one has to determine if reintroduction is a valid method in a case-by-case approach. Reintroduction might not always be possible, since adaption within the ecosystem usually leads to remaining species quickly filling the vacant niche(s) and thus reintroduction will fail or might cause other species harm.

Overview of current knowledge

When researching the keystone species concept the obvious lack of birds being the subject of relevant papers is clearly noticeable (Cronin et al., 2014). There is a clear taxonomic bias, as more than half of research concerning keystone species discussed in a recent review was dedicated to mammals (Hale & Koprowski, 2018). Mammals are viewed as ‘crowd-pleasing’ species: well-known, often scoring high in the ‘cuteness’-factor and easily visible. Therefore, mammals benefit conservation programmes, because programmes for these species can more readily acquire funding and media attention (Czech et al., 2001). This can lead to a cascading effect where less ‘attractive’ species can hitchhike with preservation measurements targeted at mammals, affecting the entire ecosystem (Clark & May, 2002). Another reason of why birds are one of the taxa least represented in these studies could be that they are a less ‘useful’ group, since few studies specifically mention bird species as keystone species. This can be due to the fact that researchers do not use the term keystone species, even though the bird species that is being studied would classify as a keystone species, as there are many studies indicating a very important role for bird species within their ecosystems. I therefore doubt that the lack of literature specifically mentioning birds as keystone species means that there are no keystone bird species. I will reason why the keystone species concept applies to more bird species than is shown.

Predators

The aforementioned grey wolves are the classic textbook example of a keystone species. Due to persecution by humans they disappeared from many of their original area and with them, the important niche they filled within the ecosystem was left vacant. Not only did they keep the populations of their prey species in check, they were an essential selection pressure in those same species (Skogland, 1989). Moreover, by inducing a landscape of fear, grey wolves caused a far-reaching change in behaviour of prey animals which causes a rippling effect throughout the ecosystem. Since the reintroduction of grey wolves in various areas, these processes have returned in full effect (Laundré et al., 2001).

This same principle applies to avian predators. Less known, but virtually identical processes can be found in several bird species. Especially birds of prey have suffered a lot from extensive hunting and usage of pesticides (Porter & Wiemeyer, 1969; Wallin, 1984). The peregrine falcon (*Falco peregrinus*) was one of the species that was hit hardest and threatened with extinction. After the ban of harmful substances such as DDT, raptor populations began to increase again, reinforced by reintroduction projects (Evans, 1982). Peregrine falcon populations benefited from this and are now thriving again (Cade et al., 1988). Analogous to grey wolves, the role of the peregrine falcon is that of the apex predator. So, do peregrine falcons also create a landscape of fear, a role attributed to keystone species? Yes, peregrine falcons not only have an effect on body mass of waders, but also affect migration behaviour as a whole (Piersma, 2003; Ydenberg et al, 2004). Waders are known to shorten their migration stopovers and alter their foraging tactics during these stopovers due to the presence of peregrines. This has a profound effect in the entire food web. Western sandpipers (*Calidris mauri*) spend less time foraging in areas with peregrine falcons, thus peregrine falcons reduce the pressure on amphipods and other prey species of these waders (Ramer, 1985). Another reintroduced raptor species causing such a cascading effect through means of a landscape of fear is the golden eagle (*Aquila chrysaetos*) (O’Toole et al., 2002; Ehmsen et al., 2011). Not only herbivorous prey species are directly affected, but indications are that mesopredators also adapt their behaviour to increased golden eagle presence. A process known as intraguild predation, where different predators not only compete for prey, but the top predator also hunts the smaller predators probably plays a part here (Lourenço et al., 2011). The overall predation of golden eagles on these mammalian mesopredators might cause a decreased predation pressure on prey species. Moreover, the location of nesting sites of golden eagles might have an impact on area usage of pine martens (*Martes martes*) (Lyly et al., 2015). Golden eagles seem to provide indirect safety for juvenile black (*Tetrao tetrix*) and hazel grouse (*Tetrastes bonasia*) through a landscape of fear effect (Lyly et al., 2016).

Regulating prey species is the other crucial role that raptors perform within an ecosystem (Donázar, 2016). From a conservation perspective, this is important as to maintain healthy populations of prey species, so diseases are unable to cause collapse of populations of prey species. Tightly linked are the Spanish imperial eagle (*Aquila adalberti)* and European rabbit (*Oryctolagus cuniculus*). Rabbits are viewed as a keystone species as they are a crucial food supply for avian predators, including the Spanish imperial eagle, a rabbit-specialist predator (Delibes-Mateos, 2007). High rabbit density equals high presence of Spanish imperial eagles and when rabbit populations plummeted during the 1950's due to infectious diseases, the eagle population also declined. However, the main causes for Spanish imperial eagle populations to be dwindling were not related to food shortage. Severe prosecution for raptor management and the collection of museum specimens, with the use of poison and gun, are the prime reasons for this near-extinction (González et al., 2008; Sánchez, 2008). The decline of rabbit populations mostly affected recovery of the Spanish imperial eagle population, causing a huge decline of reproductive success in already degraded habitat without alternative prey (Margalida et al., 2007). In fact, the low number of eagles might have enabled Myxomatosis and Rabbit Haemorrhagic Disease to be so destructive. Predators mostly predate the weaker animals because they are in principle more easily caught. This makes predators a main factor of natural selection (Götmark et al., 1997; Réale & Festa-Bianchet, 2003). A result of this lowered predation pressure by Spanish imperial eagles was a higher survival rate of rabbits, specifically weaker animals. Therefore, infected rabbits would live longer and would thus be more likely to spread the disease. Spanish imperial eagles are also known to eat carrion, so infected carcasses would linger longer in the environment. Yet, even after reintroduction of eagles in their core range (Doñana), rabbit populations were hit with disease again, causing a decline of more than 80% of rabbits in Doñana between 2012-2014 (Ferrer et al., 2013; Delibes-Mateos et al., 2014; Lopes et al., 2015). The specific interactions between these two species requires further research, but it indicates that even within a single food web there can be more than one keystone species.

Ecosystem engineers

Ecosystem engineers might be the most easily recognizable group of keystone species. The most well-known species for this category is the Eurasian beaver (*Castor fiber*). By creating their dams they actively change their surroundings and have an enormous influence on their ecosystem (Paweł et al., 2014). As a keystone species, they affect not only species living in the watercourses they dam, but also species living far away from them (Nummi & Holopainen, 2014). Beavers were almost completely gone from their original range due to relentless hunting, mostly for fur and meat, which had a profound effect on the ecosystem (IUCN, 2011). After their reintroduction in several European countries, they fill their keystone role once again (Halley & Rosell, 2002).

Woodpeckers come in at a close second as well-known ecosystem engineers (Drever et al., 2008). By drumming cavities in trees, a small adjustment to the environment, woodpeckers influence the entire food web. Sapsuckers (*Sphyrapicus*) mainly feed on sap of trees and to reach this food supply, they drill sap wells into trees. Red-naped sapsuckers (*Sphyrapicus nuchalis*) and yellow-bellied sapsuckers (*Sphyrapicus varius*) not only allow themselves to feed this way, but also hummingbirds (e.g. rufous hummingbird *Selasphorus rufus* and ruby-throated hummingbird *Archilochus colubris*), orange-crowned warblers (*Leiothlypis celata*), chipmunks (*Sciuridae*) and more sap robbers benefit (Tate, 1973; Ehrlich & Daily, 1988). Rufous and ruby-throated hummingbirds are even limited in their distribution range by the presence of yellow-bellied sapsuckers (Miller & Nero, 1983). Woodpeckers thus meet the criteria for keystone species, being exceptional in their presence relative to the rest of the community. There are some differences in the specific role woodpeckers play in an ecosystem, which is mainly due to the different behaviour between woodpecker species. Another role of woodpeckers is that of creating nesting cavities. Many species create a fresh cavity each year, to be used as nesting hole. Eurasian three-toed woodpecker (*Picoides tridactylus*) cavities provide important nesting places for secondary cavity-nesting species such as Eurasian pygmy owl (*Glaucidium passerinum*) (Pakkala et al., 2018).

Sapsuckers perform a double keystone role, since, next to their sap wells, they also create cavities in trees for nesting (Daily et al., 1993). Each year, red-naped sapsuckers create new cavities to nest in. The cavities from previous years can therefore be used by secondary cavity-nesting species such as tree swallow (*Tachycineta bicolor*) and violet-green swallow (*Tachycineta thalassina*). These two swallow species depend on these cavities for their reproduction since they do not nest anywhere else and (local) extinction of red-naped sapsuckers probably would lead to (local) extinction of these swallows.

Research has indicated that this process is currently ongoing in the system involving Red-cockaded woodpeckers (*Leuconotopicus borealis*). The cavities of this species are frequently used by secondary users (Conner et al., 1997). Birds like Eastern screech owl (*Megascops asio*) and American kestrel (*Falco sparverius*) are frequent users of the cavities, but more often Southern flying squirrels (*Glaucomys volans*) are the new inhabitants. There is even a higher level to this secondary usage. Pileated woodpeckers (*Dryocopus pileatus*) enlarge the cavities created by red-cockaded woodpeckers and these enlarged cavities also have secondary users, which are thus tertiary users. After their steep decline starting in the 1700's, only 1% of red-cockaded woodpecker's original population now remains (Ligon et al., 1986; IUCN, 2017). Recent restoration projects of the preferred habitat of red-cockaded woodpeckers have not only increased woodpecker populations but also those of other species (Wilson et al., 1995).

This is not solely due to the fact of restoring red-cockaded woodpecker populations, but one can understand that dependant species will increase once woodpeckers are able to create significant amounts of cavities again. The effects of recent reintroduction programmes have been insufficiently studied as of yet, but this information could be key in understanding the role this keystone species plays (Saenz et al., 2002; Herbez et al., 2011).

A group of birds happily using woodpecker cavities for nesting are the hornbills (*Bucerotidae*). They are also important ecosystem engineers themselves. Hornbills are so-called frugivores, dependant on fruit for their main diet. As a result of this diet, they spread seeds all throughout their territory (Holbrook & Smith, 2000). For example, Indian Great Hornbills (*Ocyceros birostris*) are responsible for dispersing seeds of 26 different plant species in the Eastern Ghats (Santhoshkumar & Balasubramanian, 2011). Together, the black-casqued hornbill (*Ceratogymna atrata*), the white-thighed hornbill (*Bycanistes albotibialis*) and the piping hornbill (*Bycanistes fistulator*) are responsible for dispersing seeds of 56 species of trees and lianas in Western Africa (Whitney & Smith, 1998). Hornbills perform a key role in the reproduction of many species of plant and are vital in keeping their environment healthy (Holbrook et al., 2002). Hornbills, like many other frugivores, are seriously endangered (Trail, 2009). This leaves several tree species at risk of extinction, because these species rely on frugivores for their primary seed dispersal (Hamann & Curio, 1999; Cordeiro & Howe, 2003).

One might argue that seed dispersal is not an active change within in the environment and it therefore does not qualify as ecosystem engineering. Actually, primates that are highly influential seed dispersers are often considered ecosystem engineers, because not all fruits are edible or reachable by every species and by reaching and eating these fruits, they alter the environment (Lambert & Garber, 1998). This applies to hornbills in the same way, as shown above, and I would accordingly argue that seed dispersal of hornbills qualifies as ecosystem engineering.

The next group of taxa also shows that it is not of structural importance that animals are actively altering their habitat to be regarded as ecosystem engineers. Seabirds are crucial in the global nitrogen and phosphorus cycles (Otero et al., 2018). This is because sea birds consume food out on the ocean and bring nutrients back to their colonies through their excretions. Seabird guano, as their faeces are called, is key for many low productivity areas, such as islands near the Gulf of California (Sanchez-Pinero & Polis, 2000). The nutrients that are still present in the guano, dropped by nesting and roosting sea birds, provide energy for varied communities of consumers. Moreover, deceased sea birds are an important food source for local scavengers. Positive effects are also shown in the reproductive success of mammals. European herring gull (*Larus argentatus*) colonies enrich the soil with their guano and this increases the nitrogen content of local plant species. Red deer (*Cervus elaphus*) foraging on these enriched plants have a higher reproductive success (Iason et al., 1986). The increase in soil nutrients by seabird colonies boosts local available resources for dibblers (*Parantechinus apicalis*) on islands in Western Australia, increasing survival of dibblers on those enriched locations (Wolfe et al., 2004).

The importance of these sea bird colonies is exceptionally noticeable when they are removed. The introduction of a predatory mammal species, the Arctic fox (*Alopex lagopus*), to the island archipelago of the Aleutians, caused serious damage to the sea bird species native to these islands. It transformed the entire ecosystem from a grassland to a tundra, depleting most of its nutrients and leaving a deprived system behind, thus causing a trophic cascade with attached secondary extinctions (Croll et al., 2005). The presence of another invasive mammal, the black rat (*Rattus rattus*), causes severe hampering of the nutrient deposition of seabirds, where rat-free islands had 251 times higher nitrogen deposition rates than those invested with rats (Graham et al., 2018). The seabird colonies also stimulate adjacent ecosystems, such as nearby coral reefs and other nearshore marine ecosystems, in addition to the island ecosystems themselves. This clearly shows that nutrient deposition is a key function of these seabirds and not only important for consumers directly depending on this food supply; disruption has far-reaching consequences for the entire environment.

Scavengers

Potentially the most underrated yet most important ecosystem service provided by birds is the one delivered by scavengers. Vultures are the best-known example of a scavenger, but also the only known obligate vertebrate scavenger (Ruxton & Houston, 2004). They are fully adapted to finding and eating dead animals (Houston, 1979). This puts them in a keystone position in the food web of the consumption of cadavers. Not only do they consume meat from the cadaver themselves, they also enable other scavengers to find and consume the cadaver (DeVault et al., 2003). This process causes energy flow to be maintained in the ecosystem, facilitating nutrient movement between food webs.

The consumption of these diseased animals makes scavengers responsible for limiting the spread of disease, by recycling entire carcasses and thus cleaning up potential infestation sites (Prakash et al., 2003). If vulture populations would have been at normal levels, the previously mentioned deadly diseases Rabbit Haemorrhagic Disease and Myxomatosis might have been halted in their spread (Prakash et al., 2003; Dupont et al., 2012; Ogada et al., 2012; Peisley et al., 2017). In regards to disease, the current decline of vultures can be a huge factor in overall human health. In India, the near-extinction of Indian (*Gyps indicus*), slender-billed (*Gyps tenuirostris*) and white-rumped vulture (*Gyps bengalensis*), can lead to an increase of rabies within the human population (Markandya et al., 2008). Through the decline of vulture populations, more food remains in the ecosystem, which is then scavenged by feral dogs. This will increase the dog populations and thus the chance of dog bites which in turn leads to an increase of rabies. Not only does this increase the overall mortality of the human population, it also causes an increased cost because of health care necessary to treat patients with rabies. One can imagine that this does not only hold true for rabies, but for other zoonoses too. Furthermore, the lack of vultures in the environment can also cause more non-zoonotic diseases to spread, such as anthrax, when rotting live stock carcasses infect water or food supplies (Swan et al., 2006). Diseases present in human remains also pose a threat in certain communities now that so few vultures remain. For example, Parsees in India and Pakistan have trouble disposing of their deceased. Before the vulture decline, the commonly named ‘Towers of Silence’, would hold the dead and allow vultures to consume them. Now, they are in desperate need for a different solution for their burials, since there are no longer enough vultures to dispose of the deceased fast enough (Parry-Jones, 2001).

It seems extremely important to reintroduce these vulture species so that they can once more fulfil their important scavenging role. Significant steps in banning specific poisons such as diclofenac and releases of captive-bred individuals have recently increased vulture populations in Southeast-Asia (Pain et al., 2008). Sadly, a thorough ‘before-and-after’ analysis has not been made during the reintroduction processes, but comparative studies would still be very beneficial in better understanding the ecological value of this greatly important category.
In Europe, vulture species have seen a similar decline, but most species are making a strong comeback, with intensive conservation efforts. This would make a good staging ground for any studies into the reintroduction of bearded vulture (*Gypaetus barbatus*), cinereous vulture (*Aegypius monachus*) and griffon vulture (*Gyps fulvus*) (Frey et al., 1995; Terrasse et al., 2004).

Discussion

Birds are a fundamental keystone in many, if not all, ecosystems this planet has to offer. There is a wide variety of bird species that, when their abundance is reduced or increased, cause cascading effects in ecosystems. The scarcity of studies on birds as keystone species seems to be an artifact of taxonomic bias in research. Avian predators, ecosystem engineers and scavengers are at least equally important in the food webs as mammals can be. This paper has shown that avian predators also cause a landscape of fear, keep mesopredators and herbivorous prey species in check and are as capable as mammals to perform these ecological services. Ecosystem engineering by birds is a critical ecological function as it is necessary for the survival of many species, not only for animals but also for plants. Woodpeckers, hornbills and sea birds are likely to be of similar importance to the functioning of ecosystems as their mammalian counterparts, like the Eurasian beaver. As scavengers, some birds species may be even more important than mammals, with vultures being the only known obligate vertebrate scavenger (Buechley & Şekercioğlu, 2016).

There are many examples of bird species performing pivotal functions within ecosystems and food webs, but research has so far failed to implement this broadly recognized concept of the keystone species for birds. When performing comparative analyses, studies on birds lacking the term ‘keystone species’ will therefore not meet the criteria and so a bias arises. This can be detrimental for conservation, when often policies and management are based on quick-scans of available research. Including the leading keywords in research important for conservation efforts is therefore vital and can enhance the position of potential species in need of protection. Yet, a concept like this should not be used as a definitive in deciding whether or not to protect a species, but should be used to convey the value of species to policy makers and governments (Cottee-Jones & Whittaker, 2012).

The keystone species concept is already suffering from a varying definition and a great amount of applications, so an argument can be made that advocating for the increased usage of the keyword ‘keystone species’ can even further lead to ‘dilution’ of the keyword (Mills et al., 1993; Hale & Koprowski, 2018). This dilution would mean that the important message behind the term keystone species diminishes. This may make the term keystone species an empty shell and turn every species into a keystone species. This is a process known as ‘the demise of a scientific term’ (Figure 2, see Appendix A), where in the end the term can apply to everything and thus to nothing at all (Hardin, 2006). The importance of the keystone species concept would then be lost. However, the value of this concept might not be the strict scientific substance per se, but the ability to quickly and effectively portray the vital ecological function of seemingly insignificant species (Barua, 2011; Cottee-Jones & Whittaker, 2012).

Throughout this entire paper, I have looked at species with either increasing or decreasing population sizes. Artificially increased population size by means of reintroduction for some species allowed for interesting studies into the specific roles of these species within ecosystems. The same applies to ecosystems where species’ numbers dwindle or where they disappear entirely from their environment. The latter is a situation in need of prevention, given the negative ecosystem consequences that the extinction of species can cause. A method of conservation used in trying to prevent these harmful consequences, restoring the environment after this damage has occurred, or to improve the functioning of the ecosystem is the reintroduction of captive-bred individuals of keystone species back into the area they disappeared from (Şekercioğlu et al., 2004; Polak & Saltz, 2011; Hale & Koprowski, 2018).

However, the question remains if reintroduction is a desired conservation method to rebuild the ecosystem. The issue with the decisions regarding reintroduction is that they are inherently subjective. What is worth protecting and which species is worth of saving are fundamental questions when considering conservation and reintroduction in particular. Considering that not all species have an equally important role within an ecosystem and resources of conservation management are finite, tough choices about which species should be conserved have to be made. It is therefore imperative to determine which species are most important for the ecosystem's health and perform a thorough comparison of the species' functioning within the ecosystem (Sarrazin & Barbault, 1996; Seddon et al., 2007).

Reintroduction might not always be possible, since adaptation is a constant in ecosystems. The ecological niche that the species in consideration of reintroduction had previously, might have already been filled by other species that is still present in the ecosystem. If this is the case, the reintroduction might actually introduce an invasive species, causing harm to the extant species. Sadly, not much research into the impact of now-extinct species on ecosystems exists. For example, the ivory-billed woodpecker (*Campephilus principalis*), one of the largest woodpeckers North-America had before it went extinct, would seem to be an ideal example of a key ecosystem engineer (Scott et al., 2008).
It would be interesting to see if pileated woodpeckers now fulfils this ecological role, since this is a smaller woodpecker species occupying a similar niche in the same habitat. However, without already existing research, this subject is intrinsically difficult to study, since extinction is not something researchers can plan.

Overall, there is an extensive amount of evidence showing that many bird species fulfil an important role in ecosystems. However, most of this evidence has been found in retrospect, after species disappeared from ecosystems. Many of these species might have been keystone species and the irreversible damage caused by their disappearance has only recently been receiving attention (Şekercioğlu et al., 2004). This indicates that research into the keystone roles species fulfil in ecosystems should receive more priority, to focus conservation on potential keystone species. As Sir David Attenborough so aptly puts it: "We only know a tiny proportion about the complexity of the natural world." This complexity plays such a huge role, especially in the keystone species complex, that we should tread carefully and prevent extinction of all species. Better safe than sorry.

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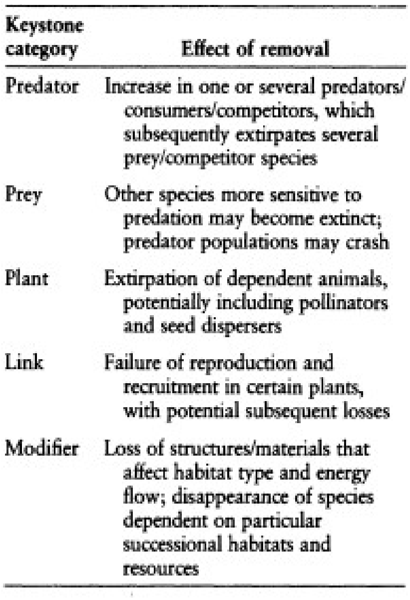
Appendix A: Supporting figures

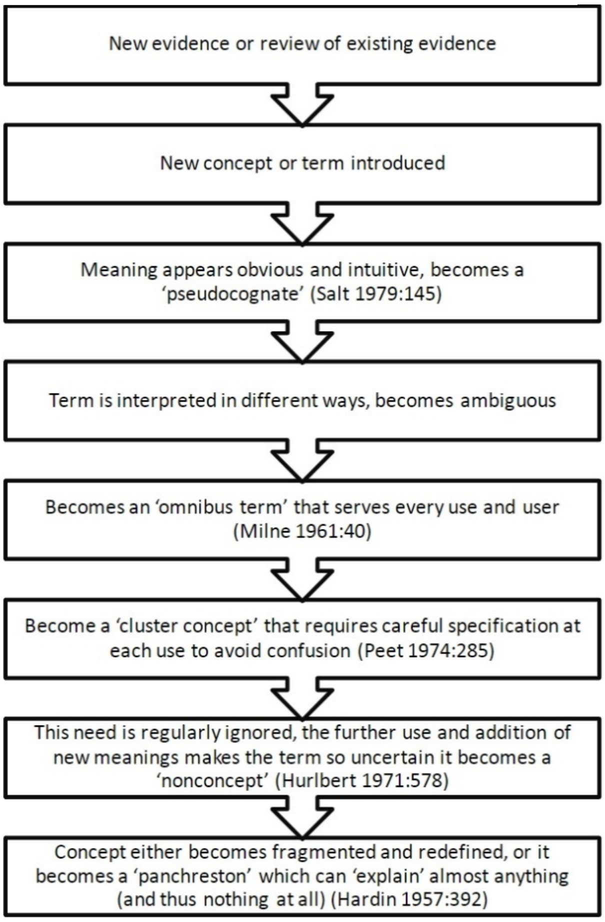
Figure 1: Overview of main keystone categories. (Mills et al., 1993)



Keystone category	Effect of removal
Predator	Increase in one or several predators/ consumers/competitors, which subsequently extirpates several prey/competitor species
Prey	Other species more sensitive to predation may become extinct; predator populations may crash
Plant	Extirpation of dependent animals, potentially including pollinators and seed dispersers
Link	Failure of reproduction and recruitment in certain plants, with potential subsequent losses
Modifier	Loss of structures/materials that affect habitat type and energy flow; disappearance of species dependent on particular successional habitats and resources

Figure 2: Process of degrading a scientific concept (Cottee-Jones & Whittaker, 2012). *Since the invention of the keystone species concept, its definition has become increasingly varied. Many reseachers have interpreted the concept in different ways, molding it to serve their specific purpose.*

Nowadays, every researcher has to explain what definition of the concept they adhere, to ensure the reader is aware of the specific definition used. This suggests that the term is already far down the track of becoming a 'panchreston', but for now still lingers in category 6.



New evidence or review of existing evidence

New concept or term introduced

Meaning appears obvious and intuitive, becomes a 'pseudocognate' (Salt 1979:145)

Term is interpreted in different ways, becomes ambiguous

Becomes an 'omnibus term' that serves every use and user (Milne 1961:40)

Become a 'cluster concept' that requires careful specification at each use to avoid confusion (Peet 1974:285)

This need is regularly ignored, the further use and addition of new meanings makes the term so uncertain it becomes a 'nonconcept' (Hurlbert 1971:578)

Concept either becomes fragmented and redefined, or it becomes a 'panchreston' which can 'explain' almost anything (and thus nothing at all) (Hardin 1957:392)