Title

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Journal

Ethics, Policy and Environment, ahead-of-print(ahead-of-print)

ISSN

2155-0093

Author

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Publication Date

2024

DOI

10.1080/21550085.2024.2389008

Peer reviewed

Taylor & Francis
Taylor & Francis Group

Ethics, Policy & Environment

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/cepe21

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ETHICS, POLICY & ENVIRONMENT
https://doi.org/10.1080/21550085.2024.2389008

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Revising the Keystone Species Concept for Conservation: Value Neutrality and Non-Nativeness

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ABSTRACT
The keystone species concept is often used in conservation. However, scientists and conservationists use the concept in many different ways. I suggest that a problem with the concept in conservation is not the lack of a shared definition. Instead, the problem is how the concept is applied to only certain species despite potentially covering a broader suite of species. This highlights unstated values in using the concept in conservation. I use novel examples, such as non-native Burmese pythons in Florida, to motivate this. I argue that the concept should include these species and be used value-neutral.

ARTICLE HISTORY
Received 16 February 2024
Accepted 31 July 2024

KEYWORDS
Keystone species; values; conservation science; environmental ethics; concepts

Introduction

The keystone species concept has been discussed in ecology and conservation for decades. These discussions range from what scientific value the term has (Mills et al., 1993), to what extent it is objective (Power et al., 1996; Valls et al., 2015), or whether it may even be just a metaphor to help people conceptualize complex ecological systems (Paine, 1995). Notably, many of the definitions offered in these papers differ (Cottee-Jones & Whittaker, 2012).

Despite these differences, keystone species are embedded within many conservation programs. For example, some state wildlife action plans in the United States use the concept to prioritize certain species for conservation.[1] The term is also used by conservation biologists or scientists, often, though not exclusively, as a focal point for conservation (c.f. Carver et al., 2021; E. E. Hart et al., 2023; Simberloff, 1998). In a conservation context, the term is often used in a positively valenced way. That is, keystone species are 'good' for conservation.

In contrast to this usage, conservationists should, as much as possible, expunge the ethical import of the concept when it is used in a conservation context. Conservation decision-makers should use the concept neutrally. One consequence is that it would include 'non-native keystone species', reflecting novel ecosystems and a changing world. This expands usage, and I will motivate this with novel examples, such as non-native Burmese pythons in Florida.

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An upshot is that this makes the concept more transparent about why certain species are keystones and are conservation priorities. Just because a species is a keystone species does not mean it is or should be a conservation priority. Still, its effects might be important once different conservation activities are agreed upon. Ideally, this improves communication between scientists, policymakers and the public and makes conservation science less prone to criticism of bias. This jointly avoids using keystone species in an unduly simplified way and highlights the specific ecological effects of particular taxa, which is paramount for reintroductions. Finally, this frontloads values and different decision-making priorities in a world of conservation tradeoffs.

Origins

Robert Paine (1933–2016) proposed the keystone species concept in his 1969 paper on intertidal communities, which builds upon his 1966 work. These papers discuss his exclusion experiments, where he experimentally removed species, such as starfish (*Pisaster sp*.), and prevented them from colonizing certain areas. Paine documented that local species diversity was directly related to the presence of starfish, a high trophic-level predator. Once the predator was removed, species diversity decreased and physical structure changed in his exclusion zones. Even though subsequent investigations (Menge et al., 1994) suggest that Paine's findings were site-specific, there was still ample evidence to generalize that some high trophic level species significantly affect the species diversity or physical structure in their ecosystems.

The concept was popular in ecology and proliferated. It was, and is, applied to a wide range of species (c.f. Shukla et al., 2023). Some of these species resemble what Paine described, but others do not (see Table 1). High trophic-level organisms are somewhat straightforward, but pollinators, plants and even guilds have been called keystones.

Table 1. Variation in the keystone species definition.

	Keystone species definition
Paine (1969)	'Within both these fairly or very complex systems the species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time, that is, stability, are determined by their activities and abundances' (92)
Power and Mills (1995)	'A keystone species is a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance' (184)
Paine (1995)	'[S]pecies that exert influences on the associated assemblage, often including numerous indirect effects, out of proportion to the keystone's abundance or biomass' (962)
Power et al. (1996)	Those species 'whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance' (609)
Simberloff (1998)	'[I]n many ecosystems, certain species have impacts on many others, often far beyond what might have been expected from a consideration of their biomass or abundance' (254)
Kotliar et al. (2006)	'[A] keystone species has unique, significant, disproportionately, large impact on its ecosystem' (61)
Delibes-Mateos et al. (2007)	'Keystone species are those considered exceptional, relative to the rest of the community, in maintaining the organization and diversity of their ecological communities' (149)
Cottee-Jones and Whittaker (2012)	'[A] species that is of demonstrable importance for ecosystem function' (125)
Carver et al. (2021)	'[O]rganisms that influence the functioning of an ecosystem disproportionate to their abundance' (1888)
Quintero et al. (2023)	Keystone species play 'important roles in ecosystem structure and function' (2)
Steenweg et al. (2023)	Keystone species have 'strong ecological impacts' (1)

In an important paper on this conceptual expansion, Mills et al. (1993) argued that the keystone species concept was poorly defined and too broadly used in ecological literature. They distinguished multiple uses of the term that identified different ecological features. For example, some papers designated a species as a 'keystone predator', which follows rather closely what Paine had in mind, but there were papers that discussed so-called 'keystone prey', which diverges from Paine's example (for a recent example, see Delibes-Mateos et al., 2007). Ultimately, Mills et al. (1993) suggested that the concept was ill-suited for ecology or conservation. They said this because it was too widely used, poorly defined, and insufficient studies showed the long-term interactions the keystone species concept should highlight. This latter problem persists, along with bias in what species are identified as keystone species, whether they are animals (Hale & Koprowski, 2018) or plants (Ballarin et al., 2023).

Following this, Power et al. (1996) proposed a definition where a keystone species is a species 'whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance' (609).[2] This definition is expansive, but it also identifies similar species to Paine (1969) and builds on a discussion from the mid-90s conference on clarifying the keystone species concept (Power & Mills, 1995). Furthermore, the definition is generally biased toward high trophic level species as they often persist in smaller numbers than other species.

However, this did not change the trend to conceptual heterogeneity despite calling for and providing a more straightforward definition. As Cottee-Jones and Whittaker (2012) note, scientists use an expansive suite of definitions. This leads to definitions picking out different kinds of organisms and ecological interactions for various reasons. Whereas one paper may use the concept for high-level predators, the concept is also used for grasses (Snyman et al., 2013), prairie dogs (Kotliar et al., 2006) or gopher tortoises (Catano & Jack Stout, 2015), all of which have different ecological effects. Cottee-Jones and Whittaker (2012) are inclusive by suggesting that 'a keystone species is a species that is of demonstrable importance for ecosystem function' (125), but this tilts toward those organisms more recently described as keystones rather than Paine's original case. A herbivorous burrowing species will affect ecosystem function differently than a generalist predator, even if they are both 'of demonstrable importance'.

The keystone species concept is used widely, and there is no definition that all practitioners use. Different species and phenomena of interest are picked out on a researcher-by-research basis. For example, some recent papers say that keystone species are species that play 'important roles in ecosystem structure and function' (Quintero et al., 2023), while others say that they are species that have 'strong ecological impacts' (Steenweg et al., 2023). While these are similar, they are not identical. To be clear, I am not suggesting these authors are wrong. Instead, this shows that the debate is not settled, and practitioners often have specific ideas and goals in mind while employing the term.

One way to respond to these debates is to throw out the concept, as it may be too vague, require a quantitative or objective metric or cover too many species. This is a mistake for several reasons. First, it can be a helpful concept for scientific communication, which I will discuss later. As Paine (1995) notes, it can shorthand complex ecological interactions, which is particularly useful when talking with the public or policymakers. Second, the concept is so widely used that discarding it seems impossible. It is used publicly, in education, and also by conservationists. Even with lingering questions, the concept covers related phenomena, which is sufficient justification for continued use.

The concept, however, ought to be revised. Just how the concept should be revised and expanded occupies the following sections of this paper. I first show the relative commonality of the keystone species concept in conservation to motivate the revision.

Conservation and Keystones

The keystone species concept is often used in conservation (Ballarin et al., 2023; Caro, 2010; Hale & Koprowski, 2018; Soulé et al., 2005). Furthermore, it is embedded within policy and is part of policy-adjacent discussion. I outline a few examples to show that, despite conceptual disagreement, it is frequently used and recommended for use in conservation.

In the United States, state wildlife management agencies create state wildlife action plans (SWAPs) in part to receive wildlife grants from the federal government. These documents explain conservation priorities, such as specific species and state agencies' goals. While there are differences on a state-by-state basis, many states utilize keystone species to orient their activities. Alaska Department of Fish and Game (2015), Colorado Department of Wildlife (2015), Florida Fish and Wildlife Conservation Commission (2019), Kenya Wildlife Service (2020a, 2020b), Maryland Department of Natural Resources (2016), Pennsylvania Game Commission and Pennsylvania Fish & Boat Commission (2015), Rhode Island Department of Environmental Management Division of Fish and Wildlife (2015), Tennessee State Wildlife Action Plan Team (2015), Utah Wildlife Action Plan Joint Team (2015), Vermont Fish & Wildlife Department (2015) and Wyoming Game & Fish Department (2015) use keystone species to varying degrees. Sometimes, this can be about highlighting certain species for conservation, such as the American beaver (*Castor canadensis*). Alternatively, the document may automatically prescribe a conservation designation to a species.[3]

Definitions of the concept, where explicit, vary from state to state; Colorado's SWAP says that a keystone species is a species that 'plays a significant role in defining the habitat in which it lives' (19). Tennessee's says they are 'species with an important role in ecosystem function' (192). Regardless of differences, keystone species are used in conservation policy in many parts of the United States.

The concept is used for conservation beyond the United States. For example, in Government of South Africa (2015), keystone species are considered 'species of special concern' in the National Biodiversity Strategy and Action Plan 2015–2025, which means they receive increased conservation prioritization (30–31). India's National Biodiversity Action Plan 2014 addendum suggests that expanding the list of keystone species is important for prioritizing conservation. This is also seen in other, more local plans. Kenya Wildlife Service's plans for Nairobi and Amboseli National Park utilize keystone species, particularly elephants.

The keystone species concept is also part of conservation policy recommendations in academic literature. For example, conservationists who support rewilding often use the concept. Carver et al. (2021) use keystone species – 'organisms that influence the functioning of an ecosystem disproportionate to their abundance' (1888) – for their first principle of rewilding. Suggestions like this are used for specific recommendations, such as rewilding in Europe (E. E. Hart et al., 2023).

These examples show that regardless of debate, the concept is often used in conservation. How it is used is variable. In some cases, the concept is frontloaded: conserve those species that are keystones for various reasons. Alternatively, some species are considered worth conserving, and their keystone effects are offered to explain why the species ought to be conserved or receive prioritization. Regardless, each direction still prioritizes some species that the keystone species concept, despite definitional differences, picks out.

However, despite this commonality, the effects of keystone species on particular ecosystems remain relatively understudied, with certain species, such as beaver or other mammals, dominating keystone restoration or reintroduction literature (Hale & Koprowski, 2018). Furthermore, even if examining ecological network strength is the right way to identify keystone species (Jordan, 2009), it is still more theoretical than practically studied. So even if there are good reasons to use keystone species for conservation or restoration, there are significant unknowns in their effects once reintroduced, how they may vary from location to location, and to what extent they are density dependent. While these are common concerns in ecology and conservation more generally, as keystone species are often used in conservation, these problems may be particularly acute.

Even with disagreement, the term is used to orient, prioritize and promote specific conservation programs. This is a mistake, and not just because people have different definitions. To make this point, I will use the definitions on offer, varied as they are, and suggest several examples that show that the concept applies to a range of unintuitive cases.

Cases

The keystone species concept has a variety of definitions. Despite this, it is often part of conservation policy and closely adjacent conservation literature. I hope to show that a problem with using the term is how it is selectively applied to only particular taxa rather than a more extensive suite of organisms that fit the definitions. This shows unstated value commitments to using the term.

I use several examples to argue for this: Burmese pythons in Florida, feral cats and rats on seabird islands. Each species exerts significant effects on ecosystem membership or functioning, which captures common usage of the keystone species concept in conservation, as previously discussed. These cases are counterintuitive to how the keystone species concept is often used, but I will motivate the examples after briefly describing them.

Pythons

Burmese pythons (*Python bivittatus*), hereafter ‘pythons’, arrived in South Florida primarily because they are popular in the exotic pet trade, facilitating an international market with animals shipped through Florida. The current population of wild pythons in Florida likely was drawn from the intentional release of juvenile and adult pet snakes in the mid-1980s near the Florida Everglades. However, due to the species’ cryptic nature, pythons were not regularly found until the mid to late 1990s (Willson et al., 2011). Knowing how many animals were imported or bred for sale as pets is unlikely to be known in fine resolution (Dorcas & Willson, 2011).

Pythons affect Florida ecosystems significantly. They do this primarily via predation. Pythons eat birds, both common and of special concern (Dove et al., 2011), mammals (Dorcas et al., 2012; McCleery et al., 2015; Taillie et al., 2021), particularly small to medium-sized mammals (Holbrook & Chesnes, 2011). Mammals, in particular, have had precipitous population declines in areas with high python densities. For example, in some locations, marsh rabbit populations have declined by over 70%, and raccoon populations appear to have fallen between 40 and 80 (Dorcas et al., 2012). Pythons may also threaten the Key Largo woodrat (Dorcas & Willson, 2011), an endangered species, and other vulnerable mammal or bird species. Furthermore, while pythons primarily eat smaller prey, larger animals such as deer or bobcats are also consumed (Bartoszek et al., 2018). Overall, there is credible evidence that python populations significantly affect the population and density of many mammal and bird species within their range.

Large-scale, indirect effects of pythons include the spread and introduction of novel parasites (Guzy et al., 2023; Miller et al., 2018), trophic cascade (Willson & Driscoll, 2017), whereby population declines of some organisms, such as raccoons and marsh rabbits, may alter ecosystem membership. Since raccoons eat many turtle eggs, their removal may increase populations of turtles or other reptiles, influencing downstream ecological membership. This may make it more likely for other non-native reptiles, such as iguanas or tegus, to take hold within the region (Meshaka et al., 2009), but it also may positively affect native reptiles.

Because pythons are top-level predators, they affect the Florida ecosystem and its ecological membership significantly despite being relatively low in number compared to other species. That said, because of how widespread they are and the difficulty in detecting them, it may be impossible to eradicate pythons in Florida (Guzy et al., 2023).

Cats

Feral cats (*Felis catus*), hereafter 'cats', are generalist predators that have spread along with humans worldwide because of their history of domestication. Cats can significantly affect a range of environments, from islands to entire continents when introduced, with some estimates suggesting cats are responsible for at least 14% of global mammal, bird and reptile extinctions (Medina et al., 2011).

That said, the species' ecological effects can vary considerably (Loss et al., 2022). Commonalities include cats preferentially preying upon and utilizing a prey subsidy with other introduced organisms, such as rabbits, where cats are present (Doherty et al., 2015; Palmas et al., 2017). When exclusion experiments were performed, trap capture rates changed for some species of Australian mammals, suggesting cats exerted significant ecological effects when present (Doherty et al., 2017).

Cat introductions can have dramatic effects in even a short period. For example, field observations showed the extirpation of rock iguanas (*Cyclura carinata*) on Turks and Caicos islands with cats and dogs over only 3 years (Alberts et al., 2002; J. Iverson, 1979; J. B. Iverson, 1978). This may have been partially caused by other kinds of human involvement, such as building development, bringing pet cats to the island, and displacement of other prey, such as rats. However, while assigning an exact causal weight is often difficult, evidence points to cats having outsized effects on environments when they are present.

Furthermore, these effects may be difficult to predict and are sometimes surprising. For example, cats may control populations of other organisms, such as rats, on seabird islands, and removing the former for conservation may cause a population change in the latter (Le Corre, 2008; c.f.; Loss et al., 2022). Regardless of the context, however, cats significantly affect the environments in which they live, such as altering species diversity, whether as a top or mesopredator.

Rats

Seabird islands are sites of conservation attention because of historical biological invasions, either intentionally or not, by a range of species, including several kinds of rats (Pacific rats, *Rattus exulans;* ship rats, *R. rattus;* Norway rats, *R. norvegicus*); I refer to these species as 'rats' for the remainder of this paper. Rats traveled the world with humans, often indirectly, and have affected nearly all terrestrial environments. Where present, they frequently have significant effects. On tropical islands, for example, rats have likely caused undocumented extinctions (Harper & Bunbury, 2015).

Rats on seabird islands have significant direct and indirect effects, even if the data is sometimes patchy (Mulder et al., 2011; Towns et al., 2006). Some direct effects include predation on seabird eggs, young birds, and even the killing of adults. In some cases, these effects on seabird populations can be dramatic, leading to extirpation (Mulder et al., 2009). However, it may also include indirect effects, including changes in the quantity of bird guano, affecting many levels of island ecosystems through reduction or changes in nitrogen provisioning (Thoresen et al., 2017). The effects on individual seabird islands and populations vary from place to place, but, at least quite often, rats significantly affect species diversity or physical structure.

Rats on some islands are high-trophic level species and may prey upon and affect seabird populations; on other islands, they may primarily be prey for other introduced animals, such as cats (Ringler et al., 2015). Furthermore, removing rats from islands has context-specific results: some examples show rapid changes (Le Corre et al., 2015), while others show rat eradication not leading to seabird recolonization (Gaze, 2000; Mulder et al., 2011). Regardless of where present, rats significantly change ecosystem function, species diversity or physical structure. While they may sometimes be quite common, it depends on the locality.

Discussion

Considering how the keystone species is often operationalized in terms of significant or disproportionate effects certain species have on an ecosystem, pythons, cats or rats on seabird islands fit these concepts. Based on the definitions, they should all be considered keystone species in their novel environments. Furthermore, these examples are generalizable to other organisms, particularly predators, that are introduced to new environments and change the environment in historically novel ways (Hobbs et al., 2009). For example, mongoose (*Herpestes javanicus*) follow similar patterns (Hays & Conant, 2007).

Table 2. Comparison of keystone species and novel examples discussed in this paper. Note that nativeness takes precedence over ecological effect in these examples.

	High trophic level relative to study site?	Ecosystem engineer?	Low number or biomass relative to the system?	Significant effect on ecosystem membership?	Native to the ecosystem?	Keystone in relevant literature?	Increases population of desirable species?
Pisaster sp.	X		X	X	X	X	X
Sea otter	X		X	X	X	X	X
Beaver		X	X	X	X	X	X
Fig tree		X	X	X	X	X	X
Python	X		X	X			X[4]
Cat	X		X	X			?[5]
Rat	X		?[6]	X			

These 'non-native keystone species' fit almost all the above definitions, which I will discuss in more detail shortly.

These examples should not imply that all or most non-native species are keystone species. Some species, such as non-native grasses like cheatgrass (*Bromus tectorum*) in the United States, are common throughout their introduced range. Therefore, that species would not fit some definitions, particularly those that require disproportionality. I visualize some of this disagreement (see Table 2) and do not necessarily see a problem with variance in different species being considered keystones under various definitions.

That said, my examples of pythons, cats and rats as 'non-native keystone species' represent a conceptual expansion, which I will discuss further in the next section. I hope to show that I have good reasons for motivating these cases. In addition, I suggest ways to rethink keystone species in conservation while accounting for these changes.

Revision

One way to think about this debate is what role the keystone species concept can or should have in conservation. For example, Mills et al. (1993) place a low value on the term, whereas others (Caro, 2010; Carver et al., 2021; Paine, 1995), perhaps with a different understanding of the term, suggest that it is useful or even central for conservation. The directions outlined by the authors stand in contrast. Of interest here is that the concept is applied to only certain species without consistency relative to conservationists' definitions.

Each of the examples provided – pythons, cats and rats – can and should be called keystone species in their introduced habitats based on at least some of the provided definitions. Each affects their environment in outsized and significant ways, such as affecting species diversity or ecological function. Were they not introduced species, each would likely be called a keystone species. This highlights ethical commitments in the concept used in conservation and adjacent fields.

To be clear, I am not suggesting that a biologist interested in using a keystone definition that focuses on 'significant effects' over a definition that uses 'low abundance' as a criterion is making a mistake. Rather, the biologists are highlighting different ecological interactions. The problem arises when it is unclear why only certain organisms are part of any keystone definition. Pythons have significant effects and have relatively low abundance, so they fit almost all definitions. In contrast, rats (and potentially cats) have significant effects but (relatively) high abundance. Some usages of the concept, particularly those that talk about significant effects, imply the inclusion of these species. However, this is not borne out in looking at relevant ecological, policy or conservation literature that uses the keystone species concept.

One way to make sense of this is that rather than a neutral description of ecological effects, such as on ecological function, physical structure or species richness, the keystone species concept, when used in a conservation context, is often employed as a shorthand among conservationists as a direction for how conservation should proceed. Conserving sea otters (*Enhydra lutris*) is 'good' because they are a keystone species; their ecological effects help restore or maintain some putatively desirable ecological features or species assemblages, namely kelp forests. Valuing specific systems, particularly historical systems, is commonly associated with using keystones (Kotliar et al., 2006) and may reflect background values favored by those biologists (Pascual et al., 2023).

These values vary, often considerably, across the conservation discipline and span from biocentric to anthropocentric. For example, Wyoming's SWAP highlights the keystone effects of domestic cattle (*Bos taurus*) while not mentioning the keystone effects of gray wolves (*Canis lupus*), which I suggest reflects the agency's broadly anthropocentric values. In contrast, mentioning sea otters as keystones often reflects biocentric 'proper function of ecosystems' values. In short, if a species is called a keystone, this often positively valences those species for conservation relative to the particular conservationist or conservation program in which the concept is embedded (c.f. Uchida et al., 2023).

However, other than Paine's (1969) definition, nativeness is almost never part of a keystone definition, and the definitions discussed are relatively minimal in carving out exceptions. In addition, most definitions have no stated ethical values, such as preferring some ecological system over another. Even when defined for their particular projects, keystone species are described in a nominally neutral manner that could include many species, including non-native ones. In practice, however, this is not the case. Keystone species are often used to foreground specific ecological processes or species assemblages over others without necessarily explaining why. Unfortunately, this can be common in conservation science and contributes to accusations of bias (Kareiva et al., 2018).

The problem, contra Mills et al. (1993) and others, is not that there is no agreed-upon definition for the keystone species concept. Often, published work, particularly on an individual species, will state explicitly why a species is considered a keystone species. Even if the justification or evidence is debatable or definitions vary, some reason is often provided. So, this is not necessarily a problem of lack of conceptual clarity. The issue is that the keystone label is applied only to certain species and not others that could fit, regardless of definition. This shows underlying ethical or value commitments in the concept as used in conservation. Furthermore, the term is not applied consistently to those species that would, under the stated requirements, fall under it. Those species omitted from consideration as keystones often have effects as significant as or even more dramatic than those in the literature. Burmese pythons are targeted for removal because of their disproportionate and significant effects, which makes them keystone species, albeit non-native ones.

I propose several points from this (summarized in Table 3). First, the keystone species concept is often considered a shorthand for 'good' conservation. Second, it is applied

Table 3. Several recommendations for making the keystone species concept more value-neutral and usable for conservation.

Recommendation	Justification	Effects
Use and identify keystone species in a value-neutral manner	As used in ecology and conservation, keystone species are not picked out equally. Definitions can be applied to a broader range of species, such as Burmese pythons, than they currently are. This is due to unstated value commitments in the concept and its usage.	Promotes value neutrality in science, which makes scientific decision-making more transparent and helps conservation science avoid accusations of bias. Expands what species are considered keystones.
Revise the keystone species concept to include 'non-native keystone species'	Species like Burmese pythons, feral cats or rats, have significant or more considerable effects in introduced environments than many already accepted keystone species. They are excluded from consideration because they are exotic.	The keystone concept is further expanded to include additional species. Reframes ecological interactions in a world of novel ecosystems, which the concept can then be used in an explanatory way to shorthand.
Keystone species should not direct conservation in policy, but they may used once conservation decisions are reached to achieve a particular goal	The keystone species concept is ill-suited to help navigate disagreements because it does not help determine what ecosystems we can or should have or value. Furthermore, pythons or sea otters may not align with what people want or what is achievable with changing environments.	Places keystone species in a subsidiary role to local or democratic decision-making. Keystone species, native or not, can still be used but are secondary to other decisions. Being a keystone species should not be a criterion in SWAPs or other conservation planning documents.

inconsistently across species, reflecting this bias. Third, the concept often obfuscates conceptual and practical disagreements, requiring change if it is going to be a conservation shorthand.

Consider sea otters again. Sea otters can significantly affect nearshore communities (Larson et al., 2014). However, those effects vary from place to place and through time (Shelton et al., 2018), and the effects might not be agreeable to a range of people. There are good reasons to believe that sea otter reintroduction in coastal California was an important part of declining abalone fisheries (*Haliotis sp.*) and may negatively affect, directly or indirectly, other fisheries or shellfish (Hines & Pearse, 1982; L. C. Hart et al., 2020; Lee et al., 2016; Watson, 2000; Wendell, 1994). Sea otter's keystone traits – high metabolism, for example – make them well-equipped to prey upon large numbers of invertebrates, not just sea urchins. While it can be argued that, overall, there are net benefits for people or improved ecosystem services as a result of their reintroduction and resumption of keystone roles (Tinker et al., 2023, pp. 96–116), it becomes a question of benefits for whom, what sort of benefits or services are measured, how benefits are distributed and who makes those decisions (Caro, 2010).

Keystone species cause significant effects, by definition. How conservationists, affected communities, stakeholders and other parties should think about this will vary considerably, particularly with sea otters reintroduced to new locations (Davis et al., 2019). The keystone species concept may communicate that some significant effect will likely occur, but not the modalities, magnitude, or how we should ethically consider it. The important tradeoffs with reintroduction or rewilding, which often frames or is in the background of keystone species discussions, are poorly served by conservation shorthand with the keystone species concept.[7] Taxonomizing the concept like Mills et al. (1993) suggest does not dissolve this either.

In response to these concerns, I suggest revising the keystone species concept following recent philosophical discussions on concepts (Plunkett & Cappelen, 2020; Wakil & Justus, 2022). The keystone species concept should be revised and used value-neutrally, capturing cases like the pythons or another species that fits under a keystone species definition. In practice, this also means recognizing what I call 'non-native keystone species'.[8] Theoretically, most of the keystone species definitions are value-neutral, so it is more a case of biologists and conservationists changing practice in using or applying the term. For example, Cottee-Jones and Whittaker (2012) definition captures the range of cases described in this paper, from the traditional (sea otters) to the novel (pythons). Similarly, Paine's original definition only requires slight modification since it identifies nativeness as a criterion.

There is much philosophical discussion about the extent that values are part of or even constitute scientific practice (Douglas, 2009; Elliott, 2017; Hicks, 2014; Schroeder, 2022; Thoma, 2024). My position here is similar to Justus (2021) and his discussion of applied ecology. The keystone species concept is suffused with thick value in much conservation literature and even in some ecological discussions. Furthermore, studies for determining species effects on an ecological community use different surrogates or statistical methods, which may indicate values in conservation science (e.g. level of risk or what P-value ought to be selected). Even the kinds of species studied may indicate research value practices. However, the stronger claim that evaluating evidence – with caveats on what counts as a source of evidence (Longino, 1990) – is necessarily value-laden need not be true. Value-neutrality toward keystone species, as suggested, includes consistent evaluation of evidence across taxa and ecological communities.[9]

There is a second component to value-neutrality with keystones and conservation. The world is changing, and novel ecological communities are common (Hobbs et al., 2009). Valuing ecosystems with historically novel species assemblages (Santana, 2022) does not necessarily preclude valuing those with more historically grounded assemblages. Instead, it requires careful evaluation of individual ecological communities, their value for people and/or conserving biodiversity, and what conservation actions are possible or desirable. For example, pythons might not be possible to remove from Florida. Thinking of them as keystone species, albeit non-native ones, might help frame evolving attitudes toward the Everglades, an exceptionally large and continually changing novel ecosystem. Appreciating or valuing novel environments is partially served by identifying non-native keystone species and expanding the usage of the concept. In this respect, valuing a wider scope of species and communities will influence epistemic value-neutrality as outlined above. Neutrality in this context means neutrality toward kinds of ecological communities: those with more historical assemblages are not automatically afforded higher value.

Following from this, and perhaps more importantly, keystone species should be decoupled from guiding or directing conservation, particularly as noted in conservation policy. For example, SWAPs should not change a species' conservation prioritization if they are a keystone. There are significant differences of opinion about how conservation can or should proceed, and the keystone species concept does a poor job of helping to navigate those disagreements. Novel or historical ecological communities may have a range of possible keystone species, and it is not evident whether only one species might perform that role or how human or ecological communities may interact with that species.[10]

Consequently, the keystone concept should be limited to an explanatory role for conservation and should not be used to change a species' conservation importance. Namely, it can show hypothesized or realized effects a species has on a specific ecological community, such as what the species does or is likely to do (e.g. sea otters will likely predate heavily on marine invertebrates). That is sufficient. Anything more, such as suggesting rewilding must include (specific) keystone species, suggesting we ought to generally conserve keystone species, or embedding keystone species in conservation policy, overstates the conservation value of the term and dislocates democratic or local decision-making on conservation matters.

Keystone species can still have a role in conservation, but it should differ from how it is often framed. Keystones may be useful once a particular plan has been decided on for a specific area and with community or stakeholder buy-in. For example, using beavers for riparian restoration or conservation can be a good idea in many parts of the United States principally because of their effects.[11] However, this places the keystone species concept in conservation as secondary to other tradeoffs rather than frontloading it in conservation decision-making. Keystone effects are set against a complex conservation background, and the keystone species concept in conservation does not, on its own, solve or shorten discussion.

One may suggest that identifying a historical or 'natural' baseline may dissolve my objection; historical baseline keystones in a particular area allow a fair selection process. I do not think this works for several reasons. First, identifying past states for comparison may use contentious selection criteria and values (c.f. Jax, 2010 for parallel discussion on ecological function). However, there are better or worse ways to do this; at least some investigation of historical baselines (e.g. paleoecology) may be about the data's adequacy for current conservation purposes (Watkins, 2024). However, as noted previously, keystone effects vary spatiotemporally: the mere presence of otters does not necessarily indicate their ecological effects. Detection of a historical organism may satisfy some purposes, but it is unlikely to give fine-grained information about how ecological communities will respond to the inclusion or exclusion of a particular organism. Looking to the past cannot entirely dissolve this problem.[12]

These suggestions aim to make the concept more transparent by making private or institutional value judgments no longer a part of the concept; keystones are not assumed to be 'good' for conservation. This value neutrality is preferable for conservation science and policy and should help avoid claims of bias.[13] Furthermore, it is meant to realign the keystone species concept to primarily an explanatory or secondary role in conservation. Pythons, cats, rats, sea otters and many other species can have significant ecological effects depending on what ecosystem they are in. These examples are worth noting and teaching, particularly in a world of novel ecosystems. However, conservationists must not let those effects overshadow conservation tradeoffs.

While looking for conservation shortcuts may be appealing – such as prioritizing a species merely because it is a keystone as some SWAPs do – it has the downside of creating conceptual or practical confusion. Aiming for more explicit values and concepts in conservation is the right decision in the long term. It makes communication among professionals, policymakers and the public more manageable and reduces the risk of accusations of bias.

Conclusion

The keystone species concept has been part of conservation decision-making for decades. The concept still has a role, but it requires revision. Applying it more broadly, as suggested here, does not dissolve disagreement. Instead, I hope these cases draw attention to the need for more value transparency in conservation and the keystone species concept. Rather than assuming keystones are necessarily 'good' for conservation, justification for conservation should depend on the specific effects, goals and possibilities of a particular locality, regardless of the keystone species under consideration. Put another way, value-neutrality toward evidence and a valuation of novel ecosystems are both outcomes of the perspective outlined here.

The role of conservation professionals and conservation science is more critical than ever. Ensuring that decisions are made as openly and clearly as possible is paramount. Like the concept itself, the keystone species' role in that future will vary from place to place. Keystone species, native or otherwise, significantly affect their ecosystems. Conservation decision-makers should consider and communicate those effects critically, clearly and fairly.

Notes

1. They may use NatureServe (https://explorer.natureserve.org/AboutTheData/DataTypes/ConservationStatusCategories) and label a species as an S3 rather than an S4, which may increase conservation attention.
2. There is a quantitative component to this definition, but that is not often used or explicitly mentioned in subsequent papers that use the keystone species concept.
3. For example, some species' S or G status – labels used by some conservation actors to reflect conservation prioritization – may change to reflect a change in priority. These designations often draw on the NatureServe system as it is adapted for SWAPs.
4. This is due to the effects on native reptiles, such as turtles.
5. This is checked insofar as cats eat rats on many islands and control their numbers, which is desirable to many.
6. The number of rats on a given island is unclear. As well, the proportional number of rats compared to birds is even less clear. However, even if there is a greater biomass of rats on an island compared to birds, that is still inclusive of keystone definitions that focus on significant effects on an ecosystem.
7. This is similar to a broader concern of the kinds of metrics used in conservation and how those may omit metrics about people (Bocchi, 2024).
8. Following Mills et al. (1993), any of their subdivisions can include non-native keystone species. This is not the only way to operationalize my recommendations, however.
9. My argument in this paper should not be construed as saying all scientific concepts can or should be value-free or even value-neutral. Instead, I am endorsing a view of values in applied ecology that are broadly political insofar as there are worries about how the concept is used

and how evidence is not used consistently across fields (Schroeder, 2022). In addition, the values in science literature constitute only one step in the process as applied to conservation. Conservation often includes scientific concepts and evidence from the sciences, but conservation is not necessarily directed by any particular scientific field or viewpoint. I'm grateful for an anonymous reviewer for discussion on this section.

10. For example, domestic cattle and American bison (*Bison bison*) can, under certain circumstances, perform similar ecological roles (Collins, 1992; Knapp et al., 1999).
11. But, even with beavers, note that their effects are noticeably different outside North America, such as in South America (Anderson et al., 2006; Henn et al., 2016).
12. I'm grateful to an anonymous reviewer for raising this point.
13. This is an empirical claim that may require investigation. I'm grateful for discussion at the 2024 Knowledge, Science, and Society conference at UCSD on this topic.

Acknowledgement

I thank Carlos Santana, Matt Haber, Joyce Havstad, Drew Dittmer, Jay Odenbaugh, and Drew Ruble for their helpful comments on this research project. I also greatly appreciate Bill Heyborne's feedback on sharpening this paper as I developed it. I also thank two anonymous reviewers for their suggestions.

Disclosure Statement

No potential conflict of interest was reported by the author(s).

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References

Alaska Department of Fish and Game. (2015). *Alaska wildlife action plan*.

Alberts, A. C., Lemm, J. M., Perry, A. M., Morici, L. A., & Phillips, J. A. (2002). Temporary alteration of local social structure in a threatened population of Cuban iguanas (*Cyclura nubila*). *Behavioral Ecology and Sociobiology*, *51*(4), 324–335. https://doi.org/10.1007/s00265-001-0445-z

Anderson, C. B., Griffith, C. R., Rosemond, A. D., Rozzi, R., & Dollenz, O. (2006). The effects of invasive North American beavers on riparian plant communities in Cape Horn, Chile: Do exotic beavers engineer differently in sub-Antarctic ecosystems? *Biological Conservation*, *128*(4), 467–474. https://doi.org/10.1016/j.biocon.2005.10.011

Ballarin, C. S., Amorim, F. W., Watson, D. M., & Fontúrbel, F. E. (2023). The use and abuse of keystone plant species in restoration practices of terrestrial ecosystems. *Restoration Ecology*, *32*(1), e14030. https://doi.org/10.1111/rec.14030

Bartoszek, I. A., Andreadis, P. T., Prokopervin, C., Patel, M., & Reed, R. N. (2018). *Python bivittatus* (Burmese python). Diet and prey size. *Herpetological Review*, *49*(1), 139–140.

Bocchi, F. (2024). Metrics in biodiversity conservation and the value-free ideal. *Synthese*, *203*(5), 145. https://doi.org/10.1007/s11229-024-04561-8

Caro, T. (2010). *Conservation by proxy: Indicator, umbrella, keystone, flagship, and other surrogate species*. Island Press.

Carver, S., Convery, I., Hawkins, S., Beyers, R., Eagle, A., Kun, Z., Van Maanen, E., Cao, Y., Fisher, M., Edwards, S.R., Nelson, C., Gann, G.D., Shurter, S., Aguilar, K., Andrade, A., Ripple, W.J., Davis, J., Sinclair, A., Bekoff, M.,. . . Noss, R. (2021). Guiding principles for rewilding. *Conservation Biology*, *35*(6), 1882–1893.

Catano, C. P., & Jack Stout, I. (2015). Functional relationships reveal keystone effects of the gopher tortoise on vertebrate diversity in a longleaf pine savanna. *Biodiversity and Conservation*, *24*(8), 1957–1974.

Collins, S. L. (1992). Fire frequency and community heterogeneity in tallgrass prairie vegetation. *Ecology*, *73*(6), 2001–2006.

Colorado Department of Wildlife. (2015). *Colorado wildlife action plan*. Colorado Department of Wildlife.

Cottee-Jones, H. E. W., & Whittaker, R. J. (2012). Perspective: The keystone species concept: A critical appraisal. *Frontiers of Biogeography*, *4*(3). https://doi.org/10.21425/F5FBG12533

Davis, R. W., Bodkin, J. L., Coletti, H. A., Monson, D. H., Larson, S. E., Carswell, L. P., & Nichol, L. M. (2019). Future directions in sea otter research and management. *Frontiers in Marine Science*, *5*, 510. https://doi.org/10.3389/fmars.2018.00510

Delibes-Mateos, M., Redpath, S. M., Angulo, E., Ferreras, P., & Villafuerte, R. (2007). Rabbits as a keystone species in southern europe. *Biological Conservation*, *137*(1), 149–156. https://doi.org/10.1016/j.biocon.2007.01.024

Doherty, T. S., Davis, R. A., van Etten, E. J., Algar, D., Collier, N., Dickman, C. R., Robinson, S., Palmer, R., Robinson, S., & Edwards, G. (2015). A continental-scale analysis of feral cat diet in Australia. *Journal of Biogeography*, *42*(5), 964–975. https://doi.org/10.1111/jbi.12469

Doherty, T. S., Dickman, C. R., Johnson, C. N., Legge, S. M., Ritchie, E. G., & Woinarski, J. C. (2017). Impacts and management of feral cats Felis catus in Australia. *Mammal Review*, *47*(2), 83–97. https://doi.org/10.1111/mam.12080

Dorcas, M. E., & Willson, J. D. (2011). *Invasive pythons in the United States: Ecology of an introduced predator*. University of Georgia Press.

Dorcas, M. E., Willson, J. D., Reed, R. N., Snow, R. W., Rochford, M. R., Miller, M. A., Meshaka, W.E., Andreadis, P.T., Mazzotti, F.J., Romagosa, C.M., & Hart, K. M. (2012). Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proceedings of the National Academy of Sciences*, *109*(7), 2418–2422. https://doi.org/10.1073/pnas.1115226109

Douglas, H. (2009). *Science, policy, and the value-free ideal*. University of Pittsburgh Pre.

Dove, C. J., Snow, R. W., Rochford, M. R., & Mazzotti, F. J. (2011). Birds consumed by the invasive Burmese python (python molurus bivittatus) in Everglades National Park, Florida, USA. *Wilson Journal of Ornithology*, *123*(1), 126–131.

Elliott, K. C. (2017). *A tapestry of values: An introduction to values in science*. Oxford University Press.

Florida Fish and Wildlife Conservation Commission (FWC). (2019). *Florida's wildlife legacy initiative*. Florida's State Wildlife Action Plan.

Gaze, P. (2000). The response of a colony of sooty shearwater (Puffinus griseus) and flesh-footed shearwater (P. carneipes) to the cessation of harvesting and the eradication of Norway rats (Rattus norvegicus). *New Zealand Journal of Zoology*, *27*(4), 375–379. https://doi.org/10.1080/03014223.2000.9518247

Government of South Africa. (2015). *National biodiversity strategy and action plan*. Department of Environmental Affairs.

Guzy, J. C., Falk, B. G., Smith, B. J., Willson, J. D., Reed, R. N., Aumen, N. G., Avery, M. L., Bartoszek, I. A., Campbell, E., Cherkiss, M. S., Claunch, N. M., Currylow, A. F., Dean, T., Dixon, J., Engeman, R., Funck, S., Gibble, R., Hengstebeck, K. C., Humphrey, J. S., & Yackel Adams, A. A.. . . Hart, K. M. (2023). Burmese pythons in Florida: A synthesis of biology, impacts, and management tools. *NeoBiota*, *80*, 1–119. https://doi.org/10.3897/neobiota.80.90439

Hale, S. L., & Koprowski, J. L. (2018). Ecosystem-level effects of keystone species reintroduction: A literature review. *Restoration Ecology*, *26*(3), 439–445.

Harper, G. A., & Bunbury, N. (2015). Invasive rats on tropical islands: Their population biology and impacts on native species. *Global Ecology and Conservation*, *3*, 607–627. https://doi.org/10.1016/j.gecco.2015.02.010

Hart, E. E., Haigh, A., & Ciuti, S. (2023). A scoping review of the scientific evidence base for rewilding in europe. *Biological Conservation*, *285*, 110243. https://doi.org/10.1016/j.biocon.2023.110243

Hart, L. C., Goodman, M. C., Walter, R. K., Rogers-Bennett, L., Shum, P., Garrett, A. D., Watanabe, J.M., & O'leary, J. K. (2020). Abalone recruitment in low-density and aggregated populations facing climatic stress. *Journal of Shellfish Research*, *39*(2), 359–373. https://doi.org/10.2983/035.039.0218

Hays, W. S., & Conant, S. (2007). Biology and impacts of Pacific Island invasive species. 1. A worldwide review of effects of the small Indian mongoose, *Herpestes javanicus* (Carnivora: Herpestidae). *Pacific Science*, *61*(1), 3–16. https://doi.org/10.1353/psc.2007.0006

Henn, J. J., Anderson, C. B., & Martínez Pastur, G. (2016). Landscape-level impact and habitat factors associated with invasive beaver distribution in Tierra del Fuego. *Biological Invasions*, *18*(6), 1679–1688. https://doi.org/10.1007/s10530-016-1110-9

Hicks, D. J. (2014). A new direction for science and values. *Synthese*, *191*(14), 3271–3295. https://doi.org/10.1007/s11229-014-0447-9

Hines, A. H., & Pearse, J. S. (1982). Abalones, shells, and sea otters: Dynamics of prey populations in central California. *Ecology*, *63*(5), 1547–1560.

Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: Implications for conservation and restoration. *Trends in Ecology & Evolution*, *24*(11), 599–605. https://doi.org/10.1016/j.tree.2009.05.012

Holbrook, J., & Chesnes, T. (2011). An effect of Burmese pythons (python molurus bivittatus) on mammal populations in southern Florida. *Florida Scientist*, 17–24.

Iverson, J. (1979). Behavior and ecology of the rock iguana Cyclura carinata. *Bulletin of the Florida Museum of Natural History*, *24*(3), 175–358. https://doi.org/10.58782/flmnh.duqm1618

Iverson, J. B. (1978). The impact of feral cats and dogs on populations of the West Indian rock iguana, Cyclura carinata. *Biological Conservation*, *14*(1), 63–73. https://doi.org/10.1016/0006-3207(78)90006-X

Jax, K. (2010). *Ecosystem functioning*. Cambridge University Press.

Jordan, F. (2009). Keystone species and food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1524), 1733–1741. https://doi.org/10.1098/rstb.2008.0335

Justus, J. (2021). *The philosophy of ecology: An introduction*. Cambridge University Press.

Kareiva, P. M., Marvier, M., & Silliman, B. R. (Eds.). (2018). *Effective conservation science: Data not dogma*. Oxford University Press.

Kenya Wildlife Service. (2020a). *Amboseli National Park conservation and management plan*. Kenya Wildlife Service. https://www.kws.go.ke/downloads/

Kenya Wildlife Service. (2020b). *Nairobi National Park management plan*. Kenya Wildlife Service. https://www.kws.go.ke/downloads

Knapp, A. K., Blair, J. M., Briggs, J. M., Collins, S. L., Hartnett, D. C., Johnson, L. C., & Gene Towne, E. (1999). The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience*, *49*(1), 39–50.

Kotliar, N. B., Miller, B. J., Reading, R. P., Clark, T. W., & Hoogland, J. L. (2006). The prairie dog as a keystone species. *Conservation of the Black-Tailed Prairie Dog: Saving North America's Western Grasslands*, 53–64.

Larson, S., James, E., Bodkin, L., & Glenn, R. V. (Eds.). (2014). *Sea otter conservation*. Academic Press.

Le Corre, M. (2008). Cats, rats and seabirds. *Nature*, *451*(7175), 134–135. https://doi.org/10.1038/451134a

Le Corre, M., Danckwerts, D. K., Ringler, D., Bastien, M., Orlowski, S., Rubio, C. M., Pinaud, D., & Micol, T. (2015). Seabird recovery and vegetation dynamics after Norway rat eradication at Tromelin Island, western Indian Ocean. *Biological Conservation*, *185*, 85–94. https://doi.org/10.1016/j.biocon.2014.12.015

Lee, L. C., Watson, J. C., Trebilco, R., & Salomon, A. K. (2016). Indirect effects and prey behavior mediate interactions between an endangered prey and recovering predator. *Ecosphere*, *7*(12), e01604. https://doi.org/10.1002/ecs2.1604

Longino, H. E. (1990). *Science as social knowledge: Values and objectivity in scientific inquiry*. Princeton university press.

Loss, S. R., Boughton, B., Cady, S. M., Londe, D. W., McKinney, C., O'Connell, T. J., Riggs, G. J., & Robertson, E. P. (2022). Review and synthesis of the global literature on domestic cat impacts on wildlife. *The Journal of Animal Ecology*, *91*(7), 1361–1372. https://doi.org/10.1111/1365-2656.13745

Maryland Department of Natural Resources. (2016). Maryland State Wildlife Action Plan.

McCleery, R. A., Sovie, A., Reed, R. N., Cunningham, M. W., Hunter, M. E., & Hart, K. M. (2015). Marsh rabbit mortalities tie pythons to the precipitous decline of mammals in the Everglades. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1805), 20150120. https://doi.org/10.1098/rspb.2015.0120

Medina, F. M., Bonnaud, E., Vidal, E., Tershy, B. R., Zavaleta, E. S., Josh Donlan, C., Keitt, B. S., Corre, M., Horwath, S. V., & Nogales, M. (2011). A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology*, *17*(11), 3503–3510. https://doi.org/10.1111/j.1365-2486.2011.02464.x

Menge, B. A., Berlow, E. L., Blanchette, C. A., Navarrete, S. A., & Yamada, S. B. (1994). The keystone species concept: Variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs*, *64*(3), 249–286.

Meshaka, W. E., Smith, H. T., Cress, H. L., Sekscienski, S. R., Mapp, W. R., Cowan, E. M., & Moore, J. A. (2009). Raccoon (Procyon lotor) removal and the rapid colonization of the green iguana (Iguana iguana) on a public land in South Florida: A conservation opportunity for the Caribbean. *Caribbean Journal of Science*, *45*(1), 15–19. https://doi.org/10.18475/cjos.v45i1.a4

Miller, M. A., Kinsella, J. M., Snow, R. W., Hayes, M. M., Falk, B. G., Reed, R. N., Mazzotti, F. J., Guyer, C., & Romagosa, C. M. (2018). Parasite spillover: Indirect effects of invasive Burmese pythons. *Ecology and Evolution*, *8*(2), 830–840. https://doi.org/10.1002/ece3.3557

Mills, L. S., Soulé, M. E., & Daniel, F. D. (1993). The keystone-species concept in ecology and conservation. *BioScience*, *43*(4), 219–224.

Mulder, C. P., Anderson, W. B., Towns, D. R., & Bellingham, P. J. (2011). Seabird islands: Ecology, invasion, and restoration.

Mulder, C. P., Grant-Hoffman, M. N., Towns, D. R., Bellingham, P. J., Wardle, D. A., Durrett, M. S., Fukami, T., & Bonner, K. I. (2009). Direct and indirect effects of rats: Does rat eradication restore ecosystem functioning of New Zealand seabird islands? *Biological Invasions*, *11*(7), 1671–1688. https://doi.org/10.1007/s10530-008-9396-x

Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, *100*(910), 65–75.

Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, *103*(929), 91–93.

Paine, R. T. (1995). A conversation on refining the concept of keystone species. *Conservation Biology*, *9*(4), 962–964.

Palmas, P., Jourdan, H., Rigault, F., Debar, L., De Meringo, H., Bourguet, E., Mathivet, M., Lee, M., Adjouhgniope, R., Papillon, Y., Bonnaud, E., & Vidal, E. (2017). Feral cats threaten the outstanding endemic fauna of the New Caledonia biodiversity hotspot. *Biological Conservation*, *214*, 250–259. https://doi.org/10.1016/j.biocon.2017.08.003

Pascual, U., Balvanera, P., Anderson, C. B., Chaplin-Kramer, R., Christie, M., González-Jiménez, D., Martin, A., Raymond, C. M., Termansen, M., Vatn, A., Athayde, S., Baptiste, B., Barton, D. N., Jacobs, S., Kelemen, E., Kumar, R., Lazos, E., Mwampamba, T. H., Nakangu, B., & Yoshida, Y.. . . Zent, E. (2023). Diverse values of nature for sustainability. *Nature*, *620*(7975), 813–823. https://doi.org/10.1038/s41586-023-06406-9

PGC-PFBC (Pennsylvania Game Commission and Pennsylvania Fish & Boat Commission). (2015). Pennsylvania wildlife action plan, 2015-2025. In C. Haffner and D. Day (Eds.), Pennsylvania Game Commission and Pennsylvania Fish & Boat Commission.

Plunkett, D., & Cappelen, H. (2020). Oxford. https://doi.org/10.1093/oso/9780198801856.003.0001

Power, M. E., & Mills, L. S. (1995). The keystone cops meet in Hilo. *Trends in Ecology & Evolution*, *10*(5), 182–184. https://doi.org/10.1016/S0169-5347(00)89047-3

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Scott Mills, L., Daily, G., Carlos Castilla, J., Lubchenco, J., & Paine, R. T. (1996). Challenges in the quest for keystones: Identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *BioScience*, *46*(8), 609–620.

Quintero, S., Abrahams, M. I., Beirne, C., Blake, J., Carvalho, E., Jr., Costa, H. C., de Paula, M. J., Endo, W., Haugaasen, T., Lima, M. G. M., Michalski, F., Mosquera, D., Norris, D., Oliveira, T., Paemelaere, E., Peres, C. A., Pezzuti, J., Romero, S., Santos, F., & Macdonald, D. W.. . . Tan, C. K. W. (2023). Effects of human-induced habitat changes on site-use patterns in large Amazonian forest mammals. *Biological Conservation*, *279*, 109904. https://doi.org/10.1016/j.biocon.2023.109904

The Rhode Island Department of Environmental Management Division of Fish and Wildlife. (2015). *Rhode Island wildlife action plan*. The Rhode Island Department of Environmental Management Division of Fish and Wildlife.

Ringler, D., Russell, J. C., & Le Corre, M. (2015). Trophic roles of black rats and seabird impacts on tropical islands: Mesopredator release or hyperpredation? *Biological Conservation*, *185*, 75–84. https://doi.org/10.1016/j.biocon.2014.12.014

Santana, C. G. (2022). The value of and in novel ecosystem(s). *Biology & Philosophy*, *37*(2), 6. https://doi.org/10.1007/s10539-022-09833-6

Schroeder, S. A. (2022). Thinking about values in science: Ethical versus political approaches. *Canadian Journal of Philosophy*, *52*(3), 246–255. https://doi.org/10.1017/can.2020.41

Shelton, A. O., Harvey, C. J., Samhouri, J. F., Andrews, K. S., Feist, B. E., Frick, K. E., Tolimieri, N., Williams, G. D., Antrim, L. D., & Berry, H. D. (2018). From the predictable to the unexpected: Kelp forest and benthic invertebrate community dynamics following decades of sea otter expansion. *Oecologia*, *188*(4), 1105–1119. https://doi.org/10.1007/s00442-018-4263-7

Shukla, I., Gaynor, K. M., Worm, B., & Darimont, C. T. (2023). The diversity of animals identified as keystone species. *Ecology and Evolution*, *13*(10), e10561. https://doi.org/10.1002/ece3.10561

Simberloff, D. (1998). Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? *Biological Conservation*, *83*(3), 247–257. https://doi.org/10.1016/S0006-3207(97)00081-5

Snyman, H. A., Ingram, L. J., & Kirkman, K. P. (2013). Themeda triandra: A keystone grass species. *African Journal of Range & Forage Science*, *30*(3), 99–125. https://doi.org/10.2989/10220119.2013.831375

Soulé, M. E., Estes, J. A., Miller, B., & Honnold, D. L. (2005). Strongly interacting species: Conservation policy, management, and ethics. *BioScience*, *55*(2), 168–176.

Steenweg, R., Hebblewhite, M., Burton, C., Whittington, J., Heim, N., Fisher, J. T., Ladle, A., Lowe, W., Muhly, T., Paczkowski, J., & Musiani, M. (2023). Testing umbrella species and food-web properties of large carnivores in the Rocky Mountains. *Biological Conservation*, *278*, 109888. https://doi.org/10.1016/j.biocon.2022.109888

Taillie, P. J., Hart, K. M., Sovie, A. R., & McCleery, R. A. (2021). Native mammals lack resilience to invasive generalist predator. *Biological Conservation*, *261*, 109290. https://doi.org/10.1016/j.biocon.2021.109290

Tennessee State Wildlife Action Plan Team. (2015). *Tennessee state wildlife action plan 2015*. Tennessee Wildlife Resources Agency.

Thoma, J. (2024). Social science, policy and democracy. *Philosophy & Public Affairs*, *52*(1), 5–41. https://doi.org/10.1111/papa.12250

Thoresen, J. J., Towns, D., Leuzinger, S., Durrett, M., Mulder, C. P., & Wardle, D. A. (2017). Invasive rodents have multiple indirect effects on seabird island invertebrate food web structure. *Ecological Applications*, *27*(4), 1190–1198. https://doi.org/10.1002/eap.1513

Tinker, M. T., Estes, A. J., Bodkin, S. L., Murray, M. J., & Hodder, J. (2023). *Restoring sea otters to the Oregon coast*. Elakha Alliance.

Towns, D. R., Atkinson, I. A., & Daugherty, C. H. (2006). Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions*, *8*(4), 863–891. https://doi.org/10.1007/s10530-005-0421-z

Uchida, K., Blumstein, D. T., & Soga, M. (2023). Managing wildlife tolerance to humans for ecosystem goods and services. *Trends in Ecology & Evolution*. https://doi.org/10.1016/j.tree.2023.10.008

Utah Wildlife Action Plan Joint Team. (2015). *Utah wildlife action plan: A plan for managing native wildlife species and their habitats to help prevent listing under the endangered species act. Publication number 15-14*. Utah Division of Wildlife Resources.

Valls, A., Coll, M., & Christensen, V. (2015). Keystone species: Toward an operational concept for marine biodiversity conservation. *Ecological Monographs*, *85*(1), 29–47.
Vermont Fish & Wildlife Department. (2015). *Vermont wildlife action plan 2015*. Vermont Fish & Wildlife Department. https://vtfishandwildlife.com/node/551
Wakil, S., & Justus, J. (2022). The 'niche' in niche-based theorizing: Much ado about nothing. *Biology & Philosophy*, *37*(2), 1–21.
Watkins, A. (2024). The adequacy of purposes for data: A paleoecological case study. *Synthese*, *203*(5), 159. https://doi.org/10.1007/s11229-024-04588-x
Watson, J. (2000). The effects of sea otters (Enhydra lutris) on abalone (Haliotis spp.) populations. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 123–132. https://ecoreserves.bc.ca/wp-content/uploads/2012/06/watson_2000_effects_of_sea_otters_on_abalone_nrc.pdf.
Wendell, F. (1994). Relationship between sea otter range expansion and red abalone abundance and size distribution in central California. *California Fish and Game*, *80*(2), 45–56.
Willson, J. D., Dorcas, M. E., & Snow, R. W. (2011). Identifying plausible scenarios for the establishment of invasive Burmese pythons (python molurus) in Southern Florida. *Biological Invasions*, *13*, 1493–1504.
Willson, J. D., & Driscoll, D. (2017). Indirect effects of invasive Burmese pythons on ecosystems in southern Florida. *The Journal of Applied Ecology*, *54*(4), 1251–1258. https://doi.org/10.1111/1365-2664.12844
Wyoming Game & Fish Department. (2015). *Wyoming wildlife action plan*. Wyoming Game & Fish Department.