

From Diversity to Disruption: Revisiting the Keystone Species Concept

by

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A Thesis Submitted in Partial Fulfillment of the

Requirements for the Degree of

MASTER OF SCIENCE

In the Department of Geography

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University of Victoria

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Abstract

The keystone species concept has been a staple of community ecology since its conception by Robert Paine in 1969. However, despite its prominence in community ecology, literature synthesizing the landscape of keystone diversity is lacking. Similarly, how keystones respond to an increasingly human-dominated world is also unknown. To address this, we created a database of keystone species identified by the literature and classified overarching patterns in keystone traits. We additionally measure the magnitude of community response associated with a keystone's extirpation or decline via human disturbances. After compiling a list of 230 animal keystones, we identified 5 distinct archetypes via a k-means clustering analysis: high trophic level (or "high level") vertebrate consumers, low-level vertebrate consumers, low level invertebrate consumers, low level invertebrate modifiers, and low-level vertebrate modifiers. We also found that communities respond to a keystone's loss with a similar magnitude whether resulting from lethal or non-lethal-caused extirpation. Finally, we found the largest community responses were elicited from small, modifier keystones. These results challenge current cultural perception of keystones as exclusively large carnivores, and instead place an emphasis on smaller, less charismatic keystones. These results, along with our novel database, can aid policymakers and scientists alike in approaching keystone conservation from a more holistic perspective.

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Acknowledgements

I would first like to thank my supervisor, Dr. Chris Darimont, for continued support and guidance throughout this project. I would also like to thank my committee members, Dr. Kaitlyn M. Gaynor, and Dr. Boris Worm for their help with statistical analysis, overall conceptualization, and draft formulation. I'd also like to give a special thanks to Dr. Mary E. Power for providing valuable feedback on multiple manuscripts. I would additionally like to thank all the members of the ACS lab for continuous moral support, draft revisions, statistical advice, data visualization and other valuable intellectual contributions. I'd especially like to thank Sharon Kay, Ali Gladwell, Persia Khan, Dylan Dando, and little Minnow for helping to create such a lovely work environment to come into every day. Additionally, I thank Emily Ning for constant moral support and guidance for my time throughout at UVic. Her unwavering support had a profound impact on my work and my time in Victoria.

Funding for this project was provided by a Raincoast Conservation Foundation Fellowship, a UVic Graduate student Award, a UVic Department of Geography Entrance Award, a John and Myrtle Graduate Scholarship, and a W.R Derrick Sewell Scholarship. I sincerely thank all my funders.

Chapter One: Introduction

Community ecology and food web ecology has expanded to encompass increasingly complex interactions over the past 50 years. Veering away from strictly predator-prey research, current community ecology now includes nuanced functional roles that branch outside of pure consumption (McGill et al. 2006). With this expanding view, we now must account not only for lethal interactions between species, but also for non-lethal interactions that can ripple up and down food webs to shape behavior and change abiotic surroundings (Werner and Peacor 2003).

This broadened view of community ecology gave rise to the idea of a “keystone species”: a species whose impact on their ecosystem is disproportionately large compared to their abundance (Power et al. 1996). While the first identified keystone species was a consumer (Sea star *Pisaster ochraceous*; (Paine 1969)), the keystone species concept has expanded to encompass many other functional roles. These roles can include keystone modifiers (Cantor and Whitham 1989), or even keystone prey (Davic 2002).

Despite extensive theoretical work, very little literature synthesizes how the keystone species concept appears in the natural world. For example, many keystone definitions disagree on the quality of data that a researcher needs to assign keystone status (Mills et al. 1993, Power et al. 1996, Davic 2002). To date, these definitions have yet to be considered collectively, and the variety of keystone traits (e.g., body size, trophic level, taxonomy, etc.) that exist remains unclear.

Additionally, literature examining keystone function in the Anthropocene is lacking. With 28% of all assessed wildlife threatened by human disturbance, it would be reasonable to expect this trend to extend to keystone species (Worm and Paine 2016, IUCN 2022). Because of

this magnitude of human disturbance, identifying any underlying factors that might make a keystone vulnerable to human disturbances would also be of great importance.

To maintain community function, it is imperative to identify keystone species and examine the human disturbances that threaten them. Our study contributes to these objectives via a k-means clustering and pattern analysis, and fixed-effects modeling. These methods allow us to i) compile a novel list of identified keystone species, ii) identify any underlying keystone “archetypes”, and iii) measure how a community responds to a human-caused keystone extirpation or decline. This project provides a much-needed resource for future keystone studies, and helps to identify especially vulnerable and vital species for conservation action.

Chapter Two: The Diversity of Keystones

Introduction

The ‘keystone species’ concept, coined by Paine in 1969, originally referred to a single species that made “great modification” to the species composition or appearance of an ecosystem. The concept has remained prominent in ecological research, education, and conservation for decades. Contemporary efforts to synthesize knowledge, however, have been limited. Multiple definitions and functions of keystone species exist, with each definition expanding the keystone species concept from predator, to include prey, ecosystem modifiers, and beyond. (e.g., (Cantor and Whitham 1989, Mills et al. 1993, Paine 1995, Power et al. 1996). However, these definitions have yet to be considered collectively. Moreover, the taxa associated with evidence for keystone species has likewise not been summarized. Meanwhile, cultural and conservation perception often focuses on a narrow view of keystones – primarily oriented towards large terrestrial carnivores. Wolves (*Canis lupus*) and other large-bodied terrestrial top carnivores are often credited with sweeping community and landscape effects via their roles as predators and imposing behavioral changes in the community (Ripple et al. 2014 *but see* Gable et al. 2020).

Against this background, we present here a comprehensive summary and descriptive analysis of keystone species, as identified by others in the relevant literature. Our objective was to synthesize the related body of work among animal taxa, focusing on documented assertions of keystone species, the traits they possess, and the responses they invoked in ecological communities. Notably, although we clearly define the criteria we use to detect relevant literature on keystones, we relied on the authors of studies to identify species as keystones. Specifically, we accepted the assertions the authors provided for keystone designation. We comment,

however, on the criteria and associated evidence these authors brought to bear in such designations. We conclude by identifying considerable variation among identified keystones, with overarching patterns that support the designation of five keystone ‘archetypes’.

Methods

Documenting keystone species identified in the literature

We conducted a systematic literature search to encompass and extract data on keystone species identified by other scientists (Moher et al. 2015). We searched Google Scholar, Web of Science, and JSTOR with the search terms: keystone species OR keystone effect* OR keystone in the title or abstract. We read the first 600 titles from each database (n = 1800), and if the title was relevant, we read the abstract. If the title or abstract included one or more of our search terms, we scanned the full publication to determine whether it met our eligibility criteria: it had to i) clearly refer to the species as a keystone or key species in the community and ii) provide primary or secondary experimental, or observational, evidence for this assertion. We included the phrase ‘key species’ in our search during this preliminary scan because some publications that the original search yielded (n =14) only provided another study for reference; in such cases, we defaulted to the cited study (that used the term ‘key species’) as a source. These originally cited studies rarely labelled the species as a keystone, and instead only stated that they were integral, or key, and rare. If a species was represented more than once, we included the study that provided empirical evidence and that was the most recent. If the paper did not meet one or more of the criteria but still referred to the species as a keystone, we performed a backwards search to attempt to identify the source paper(s) it cited in the context of referring to keystonehood. Finally,

we located additional publications not found by our search (n = 14) by inspecting titles of references within included papers (Figure 1).

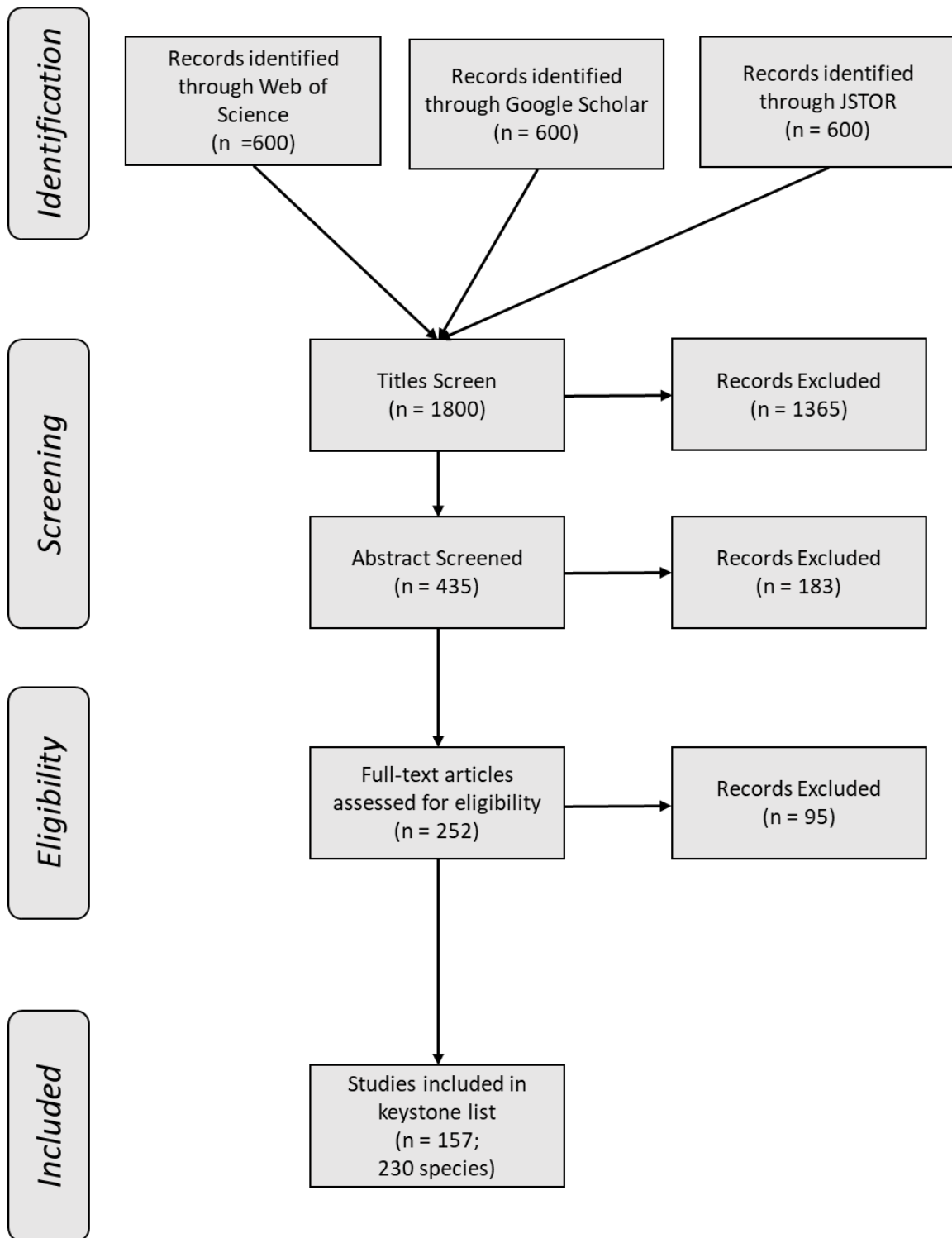


Figure 1. PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) diagram depicting the selection criteria process for documenting animal species identified as keystones in the literature.

We also categorized the rationale for keystone status provided by the authors (Figure 2). ‘Primary’ referred to any keystone identified by a study (experimental or observational) that included primary evidence of a change in community response (i.e., a significant change in abiotic or biotic factors in response to a gradient of keystone density, or presence versus absence; n = 123). ‘Primary’ also referred to a species sourced from a network analysis that found evidence of keystoneity (*sensu* Libralato et al. 2006) in which the keystoneity of a species is measured as a function of its modeled ecosystem impact relative to its biomass. A classification as ‘Post hoc’ referred to any species for which keystone status was assigned by authors after they assessed evidence from two or more empirical studies (n = 107 species). Post-hoc also included meta-analyses, studies that assign keystone status to multiple species based on multiple quantitative sources (n = 5 species; (Myers et al. 2007)).

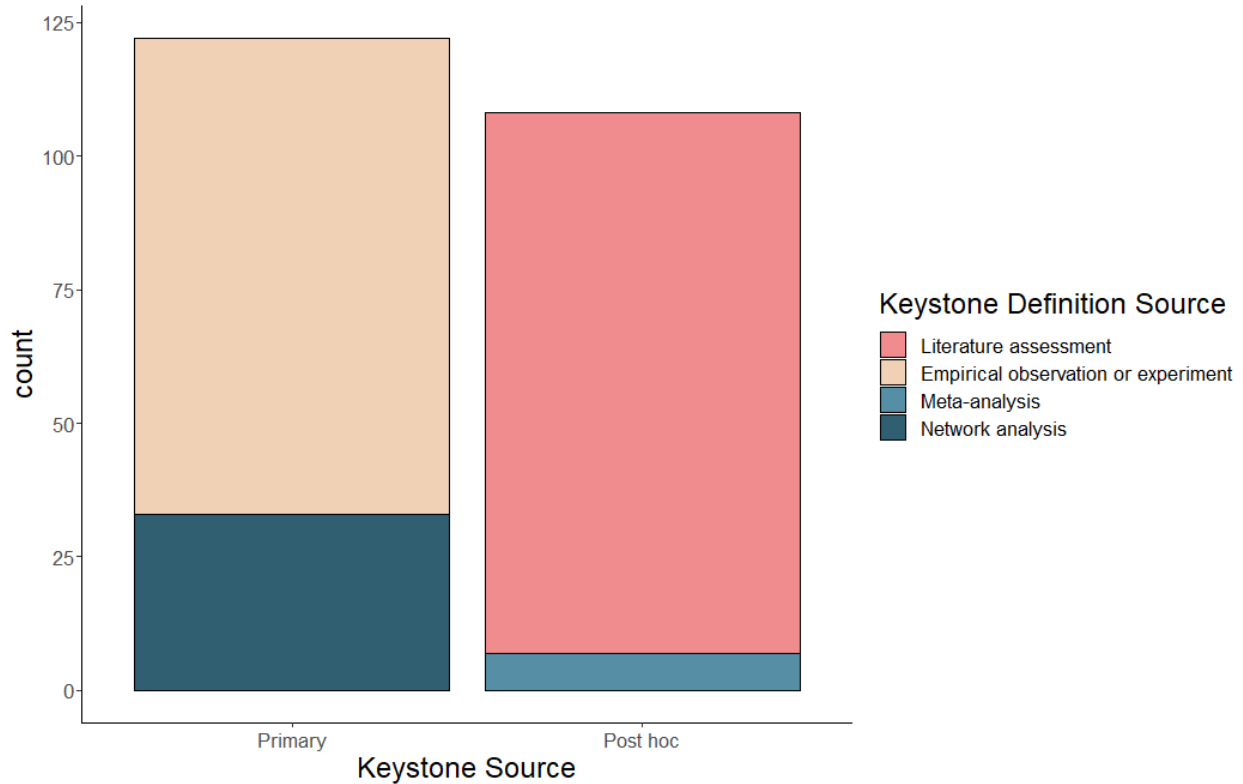


Figure 2. Justifications for keystone species as provided by authors of original studies (n = 230 species).

Data Extraction

We extracted the following data from identified studies to create a comprehensive list that we subjected to a clustering analysis informed by species’ traits and ecosystem effects. We recorded the keystone species’ role in the ecosystem (i.e. consumer, prey, or modifier), body mass, and trophic level, as well as the community response to the keystone’s absence. We also classified their habitat (aquatic or terrestrial) and taxonomic class. For simplicity, we categorized taxonomic classes *Chondrichthyes* and *Actinopterygii* as ‘fish’, *Branchiopoda*, *Insecta* and *Malacostraca* as ‘arthropods’, *Echinoidea*, *Asteroidea*, and *Ophiuroidea* as ‘echinoderms’, *Reptilia* and *Amphibia* as “herps”, and *Cephalopoda*, *Gastropoda*, *Bivalvia*, and *Polychaeta* as

“molluscs”. We classified roles as: consumer (impacts the system through consumption), prey (directly sustains one or more predator populations), or modifier (significantly alters the landscape or habitat) (Mills et al. 1993, Jones et al. 1994). We extracted average adult body mass from Fishbase, AmphiBIO, and Avonet (Froese and Pauly 2010, Oliveira et al. 2017, Tobias et al. 2022).

We assigned a concise description for each type of community response, noting if multiple responses were reported. ‘Abundance’ referred to increases or decreases in the biomass or number of other species in the community (e.g. total biomass of a prey species). ‘Behavioral’ referred to changes to behavior that alter the spatiotemporal distribution of a species (e.g. significant changes in habitat use). ‘Biodiversity’ accounted for changes to richness, diversity, or community composition (e.g. total number of species). ‘Chemical and Energy Cycling’ referred to changes to nutrient, biogeochemical, or energy cycling in the affected ecosystem (e.g. percentage of labile carbon in soil). ‘Life history’ referred to a response in growth or reproduction among other species in the community (e.g. ratio of breeding pairs, changes in body size, breeding age/rate, etc.). Finally, ‘Physical effects’ included significant physical changes to the keystone’s environment (e.g. dammed rivers, changes in sediment loads, habitat creation, etc.).

Clustering Analysis

We described patterns among keystones based on their characteristics and influence in their environments, organizing them into ‘archetypes’. Using a k-means clustering analysis, we dummy-coded species characteristics, including taxonomic class, keystone role, trophic level,

and (log standardized) body mass. For clustering analyses, we grouped herbivores, omnivores, and planktivores into a ‘low’ trophic level. Omnivores were classified as low trophic level because most were small-bodied insectivores. Mesopredators were labeled as ‘mid’ trophic level, and secondary, tertiary, and apex predators were grouped in a ‘high’ trophic level. Visual inspection using the elbow method (Kumar et al. 2022) revealed the most prominent bend at $k = 5$, identifying the optimal number of clusters (Figure S1). This method aims to identify the number of clusters (k) with the smallest sum of square distances. The smallest value (or “bend” in the graph) indicates the lowest sum of square distances. Given that this bend was not distinct, however, we also conducted multiple silhouette analyses (Kodinariya and Makwana 2013) and selected the k with the largest width and the fewest negative values. Silhouette evaluation calculates the similarity of an individual data point to its assigned cluster, as compared to the distance to the other clusters. Generally, a higher average silhouette score indicates a better clustering, with 1 indicating a perfect match, and -1 indicating a perfect mismatch. Here, an average silhouette width of 0.31 (and only one negative width) indicated the five groups provided appropriate clustering (Figure S2). Once clusters were established, we drew on the geometry of the five vectors to qualitatively describe and label each group, or ‘archetype’

Results

Our search revealed a large diversity of species identified as keystones invoking varied community responses (Table S2). Data from 157 studies led authors to designate 230 species across 17 taxonomic classes (Figure 3a). The most commonly represented classes were mammals ($n = 70$), fish ($n = 52$), arthropods ($n = 44$), and molluscs ($n = 28$). Consumers were the most common keystone roles (50%), followed by modifiers (44%), and prey (5%). Mass distribution

was highly left skewed, with a median of 431 grams and a mean of 1,862 kgs (Figure 3b). A change in the abundance of other species was the most common community response (43%), followed by biodiversity changes (19%), chemical and energy cycling (16%), changes to the physical environment (14%), changes in life history (3%), and behavioral changes (2%). Most species (70%) were associated with one community response (Figure 3c). Of the species associated with two measures, the most common additional community responses were changes in biodiversity and chemical and energy cycling (n= 23 and 21 species, respectively).

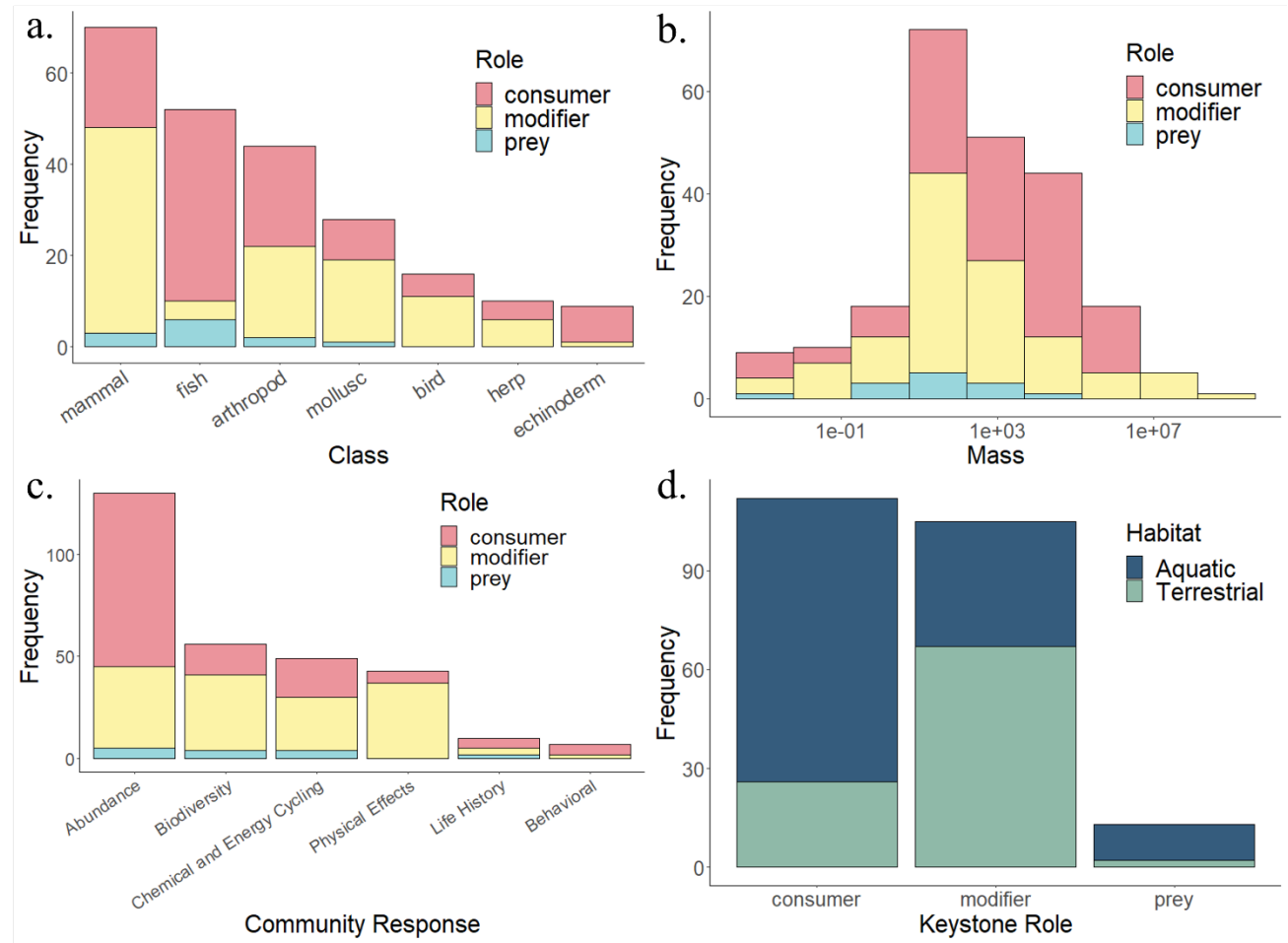


Figure 3. Distribution of keystone traits and their effects on communities and ecosystems A) Simplified taxonomic class by keystone role B) Mass by keystone role C) Community response by keystone role D) Keystone role by habitat.

Our clustering analysis revealed five distinct archetypes based on dominant traits of species and the community and ecosystem responses they elicited (Figure 4 and Table 1). Cluster 1 consisted of large-bodied, high trophic level vertebrate consumers (e.g., Bull shark, *Carcharhinus leucas*; grizzly bear, *Ursus arctos*). Cluster 2 consisted of smaller, lower-level invertebrate consumers (e.g., Long-spined sea urchin, *Diadema africanum*; cabbage butterfly, *Pieris rapae*, etc.). Cluster 3 was dominated by low-trophic level vertebrate consumers (e.g., European sprat, *Sprattus sprattus*; sheephead bream, *Diplodus puntazzo*, etc.). Cluster 4 consisted primarily of low-trophic level invertebrate modifiers (e.g., Northern shrimp, *Pandalus borealis*; common cockle, *Cerastoderma edule*, etc.). Finally, Cluster 5 was comprised primarily of low trophic level vertebrate modifiers (e.g., Greater bilby, *Macrotis lagotis*; ice rat, *Otomys sloggetti*, etc.). Clusters 1 to 3 were mostly aquatic species whereas 4 and 5 were mostly terrestrial (Table 1).

	Taxonomic class	Average mass	Trophic level	Keystone role	Habitat
Cluster 1 N = 60	54% fish 37% mammal	36.3 kg	98% high	78% consumer	76% Aquatic
Cluster 2 N = 35	61% arthropods 20% mollusc 20% echinoderms	22 g	80% low	97% consumer	78% Aquatic
Cluster 3 N = 37	66% fish 13% mammal 13% bird	416 g	86% low	89% consumer	71% Aquatic
Cluster 4 N = 40	47% arthropod, 10% mollusc, 25% mammals	18 g	97% low	95% modifier	63% Terrestrial
Cluster 5 N = 44	68% mammal	977 g	90% low	95% modifier	85% Terrestrial

Table 1. Descriptive statistics of the five keystone archetypes identified in the cluster analysis.

Only elements comprising over 10% are listed.

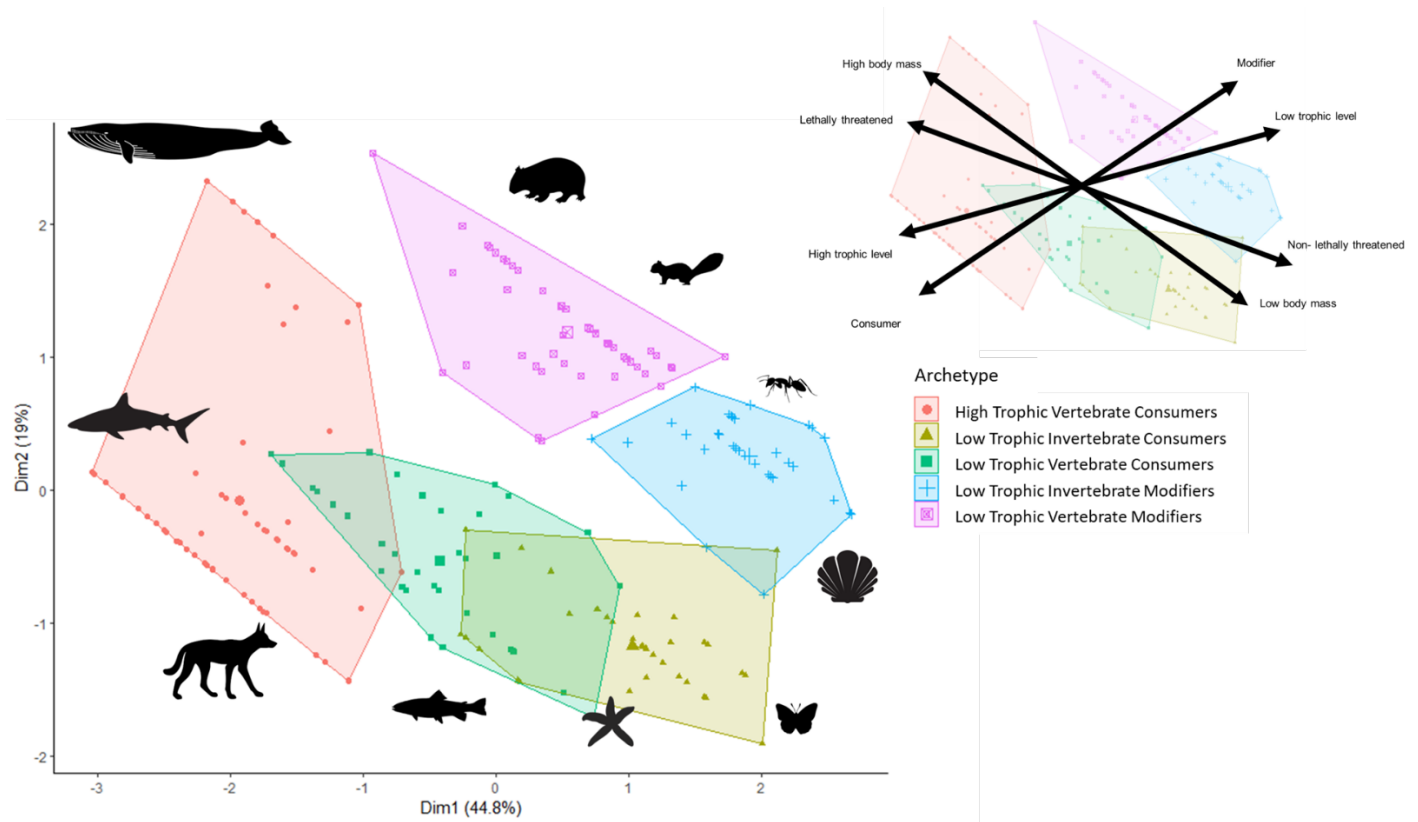


Figure 4. Five keystone archetypes as identified by a k-means clustering analysis. Axis weighting pictured top right.

Discussion

Our analysis revealed a wide range of taxonomies, roles, and community responses among species designated as keystones in the literature. Although considerable scientific and popular attention has focused on large terrestrial carnivores, the original keystone predator was a medium-sized marine invertebrate (Paine 1966, 1969), and recent research places an emphasis on keystone roles that are equally, if not more, influential than predation (Brown and Heske 1990, Brock and Kelt 2004, Davidson et al. 2012). Indeed, the subsequent literature identified many more small-bodied, low trophic level keystone species, ranging from cabbage butterfly (*Pieris rapae*) to Mole salamander (*Ambystoma talpoideum*). Current cultural perception surrounding

large carnivores might inflate the prominence of their ecosystem effects, thereby discounting smaller-bodied keystones, or those that affect ecosystems through non-trophic effects, like modifying substrates, recycling nutrients and creating habitat. Whereas consumer effects primarily elicited changes in abundance, modifier effects were far more varied (Figure 3c). Modifiers also performed multiple different ecosystem services, including energy and chemical cycling, and habitat creation, as well as affected changes in abundance (Cully Jr et al. 2010). Additionally, most keystone consumers identified here occurred in aquatic habitats, and were much more likely to be fishes (Figure 3d). Finally, most mammals identified as keystones were not consumers, but modifiers. These were primarily smaller rodents, like the Burrowing bettong (*Bettongia lesueur*), which serves as a bioturbator, altering local vegetative community composition and geochemical cycles (Davidson et al. 2012).

Although a list might suggest otherwise, keystone status should not be considered a binary designation for a species. Our list, based on 53 years of literature since the term was coined, reflected large variation in the quality and abundance of evidence for keystone justification. Our objective was neither to assess the validity of the assertions of keystone species designation, nor to evaluate the data quality or claims regarding interaction strength. Moreover, we note that the working definitions of keystone species have imprecise criteria. Only a small number of definitions provide a clear threshold for data quality (e.g. how large a “disproportionately large effect” must be, or a quantitative ratio of “community impacts” to “relative abundance”) (Power et al. 1996). Of the definitions that do provide a quantitative metric, very few subsequent keystone studies report the data required (Mills et al. 1993, Power et al. 1996). Further analysis is warranted to understand whether species designated as keystones

(and others not yet identified) indeed invoke clearly defined keystone effects on ecosystems, and how consistent those effects might be.

Despite this uncertainty, recognizing the large variation in potential keystones and their roles allows for a more comprehensive perspective on how particular species and the processes they influence might be important for conservation. We suggest that keystone identification will continue to be critical in identifying possible routes to the restoration of keystone species and their ecosystem roles (Hale and Koprowski 2018). Notably, one of the primary ways keystone species were identified was via scenarios following their extirpation or decline, and subsequent observation of how the community responded. This identification-through-loss paradigm makes the conservation of existing keystones – those known and, perhaps especially, those unknown – of critical importance.

Our list of keystones differs from those typically targeted for conservation. Most species that receive conservation funding are primarily large, charismatic vertebrates (Albert et al. 2018), yet our analysis revealed that large vertebrates represent only a modest proportion of identified animal keystones. This pattern occurred despite potential taxonomic biases in the literature, with many classes such as *Mammalia* and *Actinopterygii* appearing frequently, as opposed to relatively few studies focusing on others, such as *Gastropoda*. Most on our list are smaller-bodied and comparatively less charismatic, predisposing them to less conservation funding (Muñoz 2007). Accordingly, a new era of quests for keystones can endeavor to identify these important species before additional losses accrue.

At the intersection of the keystone species concept and human impacts is the hypothesis that humans could function as 'hyperkeystone' species (Worm and Paine 2016). Indeed, the associated hypotheses that humans ultimately elicit large community impacts via endangering

keystone species, and can do so via lethal (i.e., exploitation) and non-lethal (e.g., habitat destruction) processes, requires more detailed consideration. Ideally the list of putative species compiled here can aid in guiding such further research.

Chapter Three: The Significance of Human Disturbance on Keystone Species

Introduction

Keystone species play vital roles in influencing the diversity and function of ecosystems. A body of literature highlights the varied roles keystones serve in their communities (Crotty et al. 2020, Albuixech-Martí et al. 2021, Bensaâd-Bendjedid et al. 2022). Among the most recognizable of roles is the keystone consumer – species like sea otters (*Enhydra lutris*) and wolves (*Canis lupus*), for example, that regulate urchins (Genus) and ungulates (family), respectively, thereby influencing not only primary producers but also other species (Estes et al. 1978, McLaren and Peterson 1994) (Figure 5). Many similarly large-bodied, charismatic predators are associated with keystone community responses to such an extent that some assert that all large predators are keystone consumers (Ucarli 2011, Ripple et al. 2014).

Large predators and other consumers, however, encompass just one type of keystone role among several (Figure 5). Keystone modifiers, for example, can cause community responses by modifying the physical habitat, often via biogeochemical cycling (Mills et al. 1993). Such bioturbation can then affect biodiversity, rippling up the food web. For example, Plateau pika (*Ochotona curzoniae*) burrowing can influence plant community composition and diversity (Smith and Foggin 1999). Likewise, kangaroo rat (*Dipodomys ordii*) burrows alter the amount of

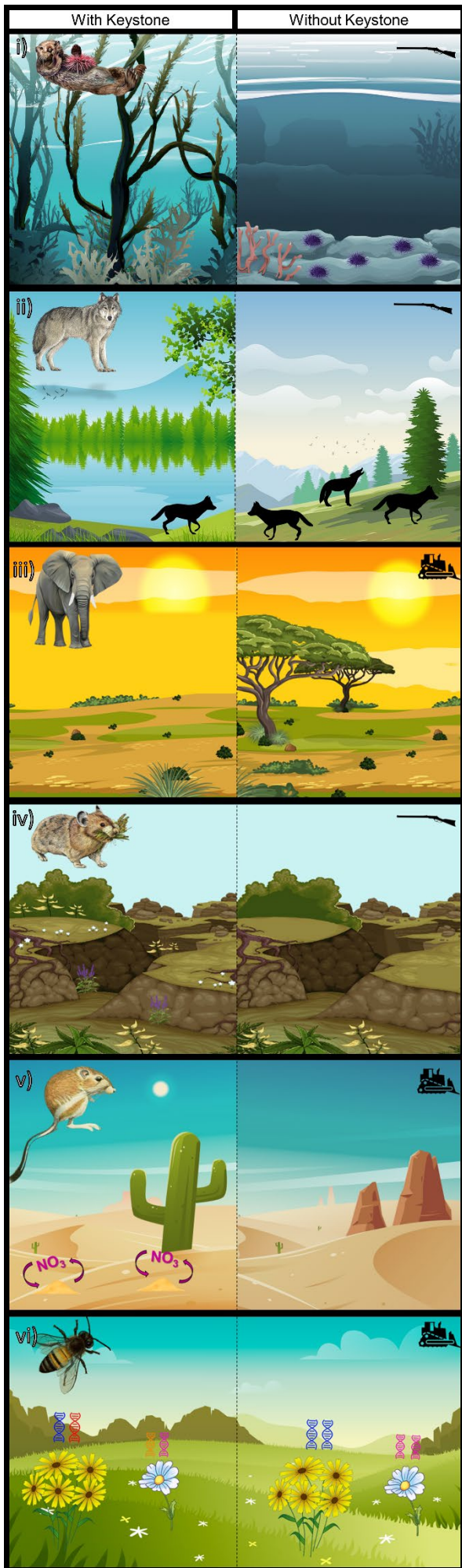


Figure 5. Examples of where human-induced keystone extirpations or declines elicit strong community responses. Gun and bulldozer icons in the top right represent lethal and non-lethal human disturbances, respectively. i) When sea otters *Enhydra lutris* were extirpated, the **abundance** of sea urchins *Strongylocentrotidae* spp. increased dramatically, overgrazing kelp forests (Estes et al. 1978) ii) After wolf *Canis lupus* extirpation, coyotes changed their **behavior** and expanded their spatiotemporal distribution (Levi and Wilmers 2012) iii) Elephants, *Loxodonta africana*, suppressed fire and maintained a grassland habitat, and these **physical effects** to the landscape were reversed when elephants declined (Dublin et al. 1990). iv) When the plateau pika, *Ochotona curzoniae*, was poisoned in pest-killings, local **biodiversity** decreased. (Harris et al. 2014). v) Kangaroo rat, *Dipodomys ordii* burrows create **chemical and energy cycling** in the desert, but effects declined where populations were low, owing to habitat fragmentation (Kerley et al. 1997). vi) Honeybee, *Apis mellifera*, pollinations alter the genetic makeup and **life history traits** of breeding flowers, but these effects are reversed where bee populations are declining due to habitat loss (Traveset et al. 2017).

labile carbon and nitrogen available to plants (Kerley et al. 1997) (Figure 5). In addition to modifiers, keystone prey directly support one more specialized predators (Mills et al. 1993). For instance, European rabbit (*Oryctolagus cuniculus*) populations directly support two specialist predators, the Iberian lynx (*Lynx pardinus*) and the Spanish Imperial eagle (*Aquila adalberti*; Monterroso et al. 2016).

These varied roles among keystones often have been identified in contexts of human disturbance. In other words, much insight has occurred in assessing community responses in comparing contexts in which keystones were present and absent or in decline (Figure 5) (Hale and Koprowski 2018, IUCN 2022). For instance, for both sea otters and wolves their keystone status was discovered after lethal forms of disturbance leading to extirpation (and/or reintroduction and recolonization) and the documentation of large associated community responses in ecosystem (Estes et al. 1978, Ripple and Beschta 2004)(Figure 5).

Against this background of human disturbance, Worm and Paine (2016) conceived of humans as a special form of keystone -- a “hyperkeystone” species. The hypothesis suggests that humans, via their disturbances of keystones, ultimately exert large responses in ecological communities, in some cases leading to ecosystem collapse (Worm and Paine 2016). They also make two important general predictions, not yet subject to empirical inquiry. One, keystone extirpations are triggered by not only lethal but also non-lethal disturbances, like habitat destruction and climate change. We assess the evidence for these scenarios, as well as compare community responses under lethal and non-lethal disturbances (while also accounting for keystone role, trophic level, and body size). Two, Worm and Paine (2016) suggested that humans substantially threaten keystone species. We likewise evaluate the evidence for this general

prediction and detail the specific threats as well as describe patterns endangerment status using data from The International Union for Conservation of Nature (IUCN) data.

Methods

Sources of data

To quantify responses of communities to the absence of or reduction in populations of keystone species, we inspected papers from a database on species identified as keystones by authors of primary research (*Shukla et al. in revision*). Briefly, from this database we selected studies with the following criteria: the publication i) employed an experimental, observational, or comparative design that ii) quantified the effects of the putative keystone species on their community via comparisons across a gradient of density or presence/absence of keystones. In 4 cases where there were multiple papers with the same focal species, author, study location, and measured community response(s) within a range of 5 years, here we selected only the most recent published paper. We only included studies with observational or experimental evidence and did not include any approaches using modelling or network analyses.

Types of community responses varied widely, and we assigned a concise description of the community responses. Responses related to ‘biodiversity’ included changes in richness, diversity, or community composition. ‘Physical Effects’ included physical changes to the keystone’s environment (e.g., number of dammed rivers, fire suppression, etc.). ‘Life history’ included any response in another organism’s vital rates, such as growth or reproduction (e.g. ratio of breeding pairs, changes in body size, breeding age/rate, etc.). ‘Behavioral changes’ included changes to the spatiotemporal distribution among other species in the community (e.g.

avoidance behavior, reduced activity, etc.). ‘Abundance’ referred to any changes in another species’ total biomass. Finally, ‘Chemical and Energy Cycling’ referred to any changes to measures of nutrient, biochemical, geochemical, or energy cycling.

Data Extraction

Disturbance Contexts

We extracted human disturbance contexts (e.g. lethal or non-lethal disturbances impacting keystone species) at the species-level from the study when provided. If no disturbance context was stated, we used the top threat across the keystone species’ range as reported in the IUCN Threat Database (IUCN 2022). If the top threat was not reported (n = 14 cases), we extracted information from the accompanying descriptive paragraph and manually characterized the threat according to the IUCN threat categories (e.g. Agriculture and aquaculture, Biological resource use, etc.)

Threat Status

We similarly extracted information on keystone species threat status from the IUCN Red List (IUCN 2022). To simplify, we separated threat status into ‘Not Threatened’ (*Least concern* and *Near Threatened*) and ‘Threatened’ (*Vulnerable*, *Endangered*, and *Critically Endangered*; Darimont et al in press).

Keystone Role

We determined a species' keystone role from each article individually. We characterized keystone roles into three categories: consumer, modifier, and prey (Mills et al. 1993).

'Consumers' referred to any species that altered ecosystem function via consumption (Paine 1969). 'Modifiers' were species that caused significant biotic or abiotic change to the physical landscape (e.g., bioturbation, tree excavation (Cantor and Whitham 1989)). Finally, 'prey' referred to any species whose populations directly supported two or more specialized predators (Davic 2002).

Mass

We sourced body mass data (average adult mass between sexes) for each keystone from amphibiO (Oliveira et al. 2017), AVONET (Tobias et al. 2022), and Fishbase (Froese and Pauly 2010). For keystones without mass data in these databases (n = 38), we searched for a peer-reviewed article with the most citations that reported body mass from Google Scholar and Web of Science.

Community Responses

Community response(s) were both biotic (e.g., zooplankton biomass, coyote habitat use, etc.) and abiotic (e.g., bare ground cover, nitrogen ratio in soil, etc.). We extracted the magnitude of responses across systems of keystone absence vs presence, as well as in systems of varying keystone. In contexts of density gradients, we selected the extreme ends of data ranges. If numerical estimates were not provided (n = 69 of 110 cases), we extracted them with WebPlotDigitizer (Rohatgi 2022). Given the broad range in measures of community response, we standardized effect sizes by computing the log response ratio between the two community states:

$$RR = \ln(X_A/X_B)$$

where X_A = the community response in the absence (or reduced density) of the keystone, and X_B = the community response in the presence of the keystone. We then used the absolute value of RR. If a study reported multiple community responses across carnivores, herbivores, plants, and abiotic material (n = 25 of 110 cases), we considered each response as a case in the analysis (e.g., a wolf eliciting a decrease in moose abundance and an increase in fir tree growth). However, if multiple counts of community response were reported in the same trophic level (i.e., measures of diversity *and* richness), we averaged these values into a single sample, reasoning that multiple community responses from the same abiotic or biotic level would be considered pseudo-replicated.

Statistical Analysis

To examine the potential influence of disturbance context, trophic level, keystone role, and body mass on the magnitude of community response, we considered a number of candidate models *a priori*. Specifically, we predicted that larger bodied keystones would elicit a stronger cumulative community response, as they can affect multiple trophic levels, possibly including a trophic cascade (Terborgh and Estes 2013). Additionally, we predicted that non-lethal disturbance contexts would not be significantly different from lethal contexts. As Worm and Paine (2016) argued, even though non-lethal disturbances are less targeted to keystones than lethal disturbances, they are generally spread across a larger area, possibly affecting a greater number of species. We also considered multiple interaction terms. We hypothesized that the effects of body mass would depend on trophic level, considering, for example that large-bodied, high-trophic level species can exert strong top-down effects (Ripple et al. 2014) but might not

be the case for smaller consumers. Similarly, we hypothesized that keystone role might depend on trophic level, given that lower-trophic-level modifiers might elicit a large bottom-up response (Davidson et al. 2012). Finally, we considered that trophic level might depend on disturbance context, as high-trophic-level species threatened by non-lethal disturbances could elicit a particularly large community response via behavioral shifts (Gaynor et al. 2018, Van Scoyoc et al. 2023). We tested for collinearity between predictors with a variance inflation factor test (VIF). With VIF values ranging from 1.1-1.5, we found an absence of collinearity (Figure S5). We then generated candidate models that included the effects of these predictor variables on RR, and evaluated the parsimony of candidate models using AIC values (Symonds and Moussalli 2011) (Table S1). We selected our top performing model based on the lowest AIC value.

We first constructed each candidate model as a mixed effects model using *glmmTMB* in R (Brooks et al. 2017; R Core Team 2021), with a gamma parameterization, best estimated with the *fitdistrplus* package (Delignette-Muller and Dutang 2015). We reached a singular fit, however, given that the only two potential candidate variables for random effects (study id and species id) generally only had one sample per level; accordingly, we then considered fixed effects models (Oberpriller et al. 2022). We excluded studies (n = 73 of 184 original studies) with keystone species with a ‘data deficient’ IUCN threat status, given that disturbance context served as a key predictor relating to our hypothesis. We also used the log transformation for body mass given the pronounced range (0.4 mg to 190,000 kg).

Results

Keystone species spanned a wide variety of disturbance contexts, threat status categories, and roles, with important patterns in how these variables interacted (Figure 6). Lethal and non-lethal disturbances were roughly equally represented (48 vs 52% of keystones, respectively). Notably, keystone species disturbed by non-lethal disturbances were more likely to be threatened (50%) than those subject to lethal disturbance (Figure 6). All those keystones with modifier roles that were threatened by non-lethal disturbances ($n = 13$) were listed as threatened (Vulnerable to Critically Endangered; Figure 6).

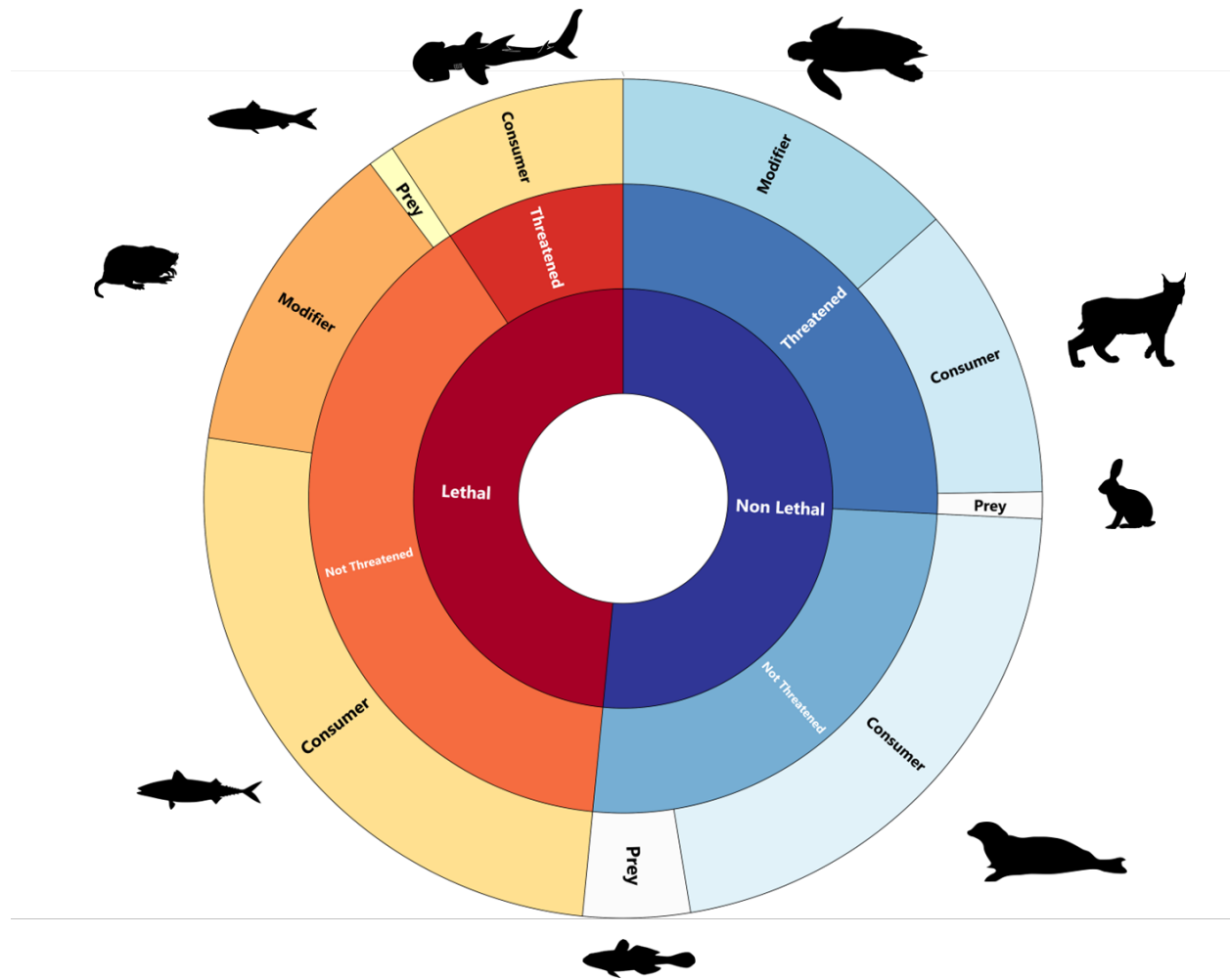


Figure 6. Keystone disturbance contexts, threat statuses, and roles of documented keystone species ($n = 97$). Example silhouettes of each pathway are provided on the outside of the ring.

The magnitude of community response varied by disturbance context, keystone role, trophic level, and body mass (Figure 7). The top model (the full model without any interaction terms) accounted for ~ 9% of variation, clearly outperformed others (Table S1). However, the directionality of each predictor stayed constant across the other, out-performed models. In models that included interaction terms, the magnitude of each predictor was muted. We observed that higher trophic levels were associated with a larger community response compared to lower trophic level keystones, but parameter coefficients overlapped zero. However, we found that modifiers and prey elicited a significantly larger community response compared to consumers. In agreement with our hypothesis, non-lethal disturbance contexts elicited a similar magnitude of community responses as lethal contexts. Additionally, contrary to our hypothesis, we found that body mass showed a negative association with magnitude of community response. Each additional unit of standardized mass was associated with a 12% (CI: 6-18%) decrease in community response.

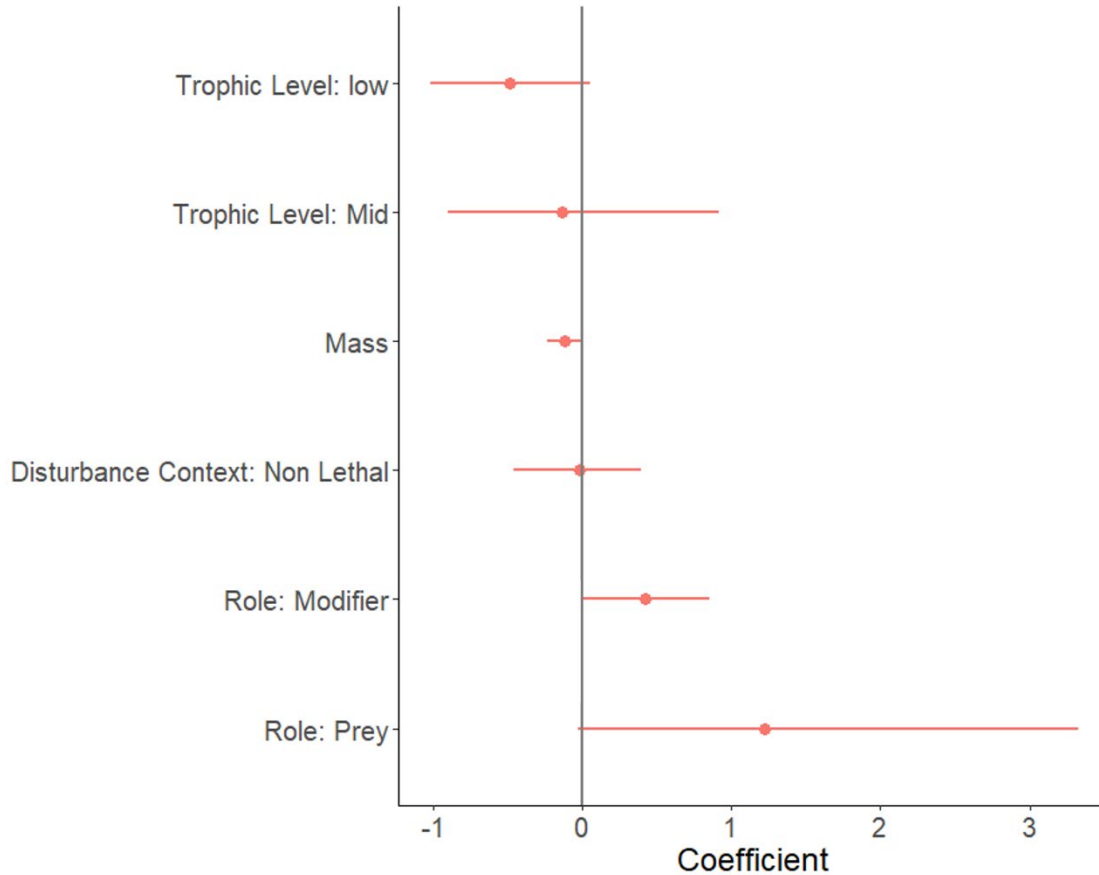


Figure 7. Parameter coefficients and 95% CIs for the fixed effects model (keystone species characteristics) explaining variation in magnitude of community response elicited by keystones.

Discussion

Our assessment revealed a variety of keystone roles, and a pronounced diversity in the types and magnitude of community responses to their absence or decline as caused by both lethal and non-lethal human disturbance. Such patterns diverge from the most commonly acknowledged role of keystones as consumers (Ripple and Beschta 2004, Ucarli 2011), the prominently considered community responses associated with consumption (i.e., changes in abundance of prey), and the lethal human processes (i.e. exploitation) that reveal the community

effects (Estes et al. 2011). Acknowledging the large breadth of keystone species, roles and community responses provides important background to consider how human disturbances affect not only keystones but also a wide variety of ecological processes.

We found that non-lethal human disturbances to keystones are common and exerted large community responses (Figure 7). Furthermore, non-lethal disturbances were common, being documented in slightly more contexts than lethal disturbances (Figure 6). Unlike the trophic changes to abundance that lethal disturbances tend to create, non-lethal disturbances can cause strong non-trophic changes in behavior, which can then in turn ripple into the community (Worm and Paine 2016). These non-trophic behavioral changes can include changes to foraging preferences, movement, and amount of activity spent in vigilance (Wilson et al. 2020). Despite the well-documented community impacts of non-lethal disturbances, lethal disturbances remain more frequently documented, possibly because the effects of non-lethal disturbances are more difficult to detect and often require longer periods of observation (Worm and Paine 2016, Werner and Peacor 2003). These less apparent non-lethal disturbances coupled with the readily observed lethal disturbances reveal contexts that could make keystones vulnerable to human disturbance.

Our analyses identified humans as a significant threat to keystones. Over a third of documented keystones are threatened by human disturbance, which is slightly higher than all assessed species (28%) (IUCN 2022) (Figure 6). Contrary to prominent keystone species paradigm (consumer keystones threatened by lethal human disturbance), we identified more consumers threatened by non-lethal disturbances than lethal disturbances (Figure 6). These disturbances often included landscape change, such as habitat fragmentation or agricultural practices. Large-bodied consumers are more likely to have larger home ranges, which increases

their need for land and their risk to exposure (Hill et al. 2020). Modifiers were even more commonly threatened by non-lethal disturbance. Indeed, all documented modifiers were threatened by non-lethal disturbances (Figure 6). Much like large consumers, the primary non-lethal threat included landscape modification. In this case, small-bodied modifiers were threatened by these fragmentation and agricultural disturbances likely because of their small home ranges and decreased mobility (Santini et al. 2019).

We also found that the community responses elicited by keystone extirpations via non-lethal means were not significantly different from community responses from keystone extirpations via lethal means. These keystone extirpations ripple throughout the community, and interfere with many important ecosystem functions and services (Figure 5). While community responses to various keystone traits might differ in magnitude, keystone loss can drastically decrease an ecosystem's productivity and resilience (Traveset et al. 2017). Our results suggest that humans increase the frequency and magnitude of these community responses and subsequent functional losses via keystone extirpation.

While accounting for other factors that can influence community response, we found that small-bodied modifiers exert especially large community responses. This further contrasts with the common perception that keystones are large consumers that caused trophic cascades via changes to abundance. Small-bodied modifiers elicited multiple community responses in their absence or decline, most often chemical and energy cycling and changes to biodiversity (Figure 7). Small modifiers (like prairie dogs *Cynomys spp.*, or kangaroo rats *Dipodomys spp.*) act as bioturbators that churn up soil when foraging or burrowing. This perturbation not only draws up and cycles important nutrients, but also acts as a form of intermediate disturbance – diversifying

the local vegetation. These effects can then ripple up the ecosystem via bottom-up interactions (Lai and Smith 2003, Brock and Kelt 2004, Cully et al. 2010).

Paradoxically, many of the important actions that keystones perform are the same reasons they are persecuted. Bioturbation often interferes with agriculture, so many small mammal modifiers are targeted as pests (Davidson et al. 2012). Similarly, many large carnivores, which keep prey in check, are targeted because of concerns over prey abundance or in retaliation killings for perceived hunting of livestock (van Eeden et al. 2018)

In the broader context, our ability to identify keystones has occurred after their loss and/or restoration. For example, we only realized the ecosystem impacts and keystone status of large carnivores after their targeted extirpation and decline (Ripple et al. 2014) or via their reintroduction (Hale and Koprowski 2018). While small modifiers are not yet in decline like many carnivorous species, anticipated increases in food production might place small modifiers in a vulnerable position (Davidson et al. 2012). Learning from the widespread extirpation of large carnivores, we must address humanity's status as hyperkeystone species and invest conservation focus on this targeted modifier group before we risk the diminished roles associated with this other important group of keystones.

Chapter Four: Conclusion

Our study reveals a wide variety of identified keystones, as well as a variety of disturbances threatening them. We found that keystones often thought of as “pests” serve a vital role in ecosystem function, oftentimes even more than their large-bodied counterparts. With this knowledge, researchers can expand conservation efforts to encompass a more realistic depiction of keystone species. In order to identify anthropogenic threats to keystone species, we first had to identify the species themselves, and while definitions and data collection methods varied between studies, we offer our list as a starting point for additional keystone research in the future.

Our study draws a closer eye to the very nature of the keystone species concept. Whereas the definition stated by Power et al. (Power et al. 1996) is the most often cited, field studies often instead rely on a qualitative assessment of keystone status based on the quantitative data they collect (Figure S2). Based on this variety between studies, we relied on author justification for keystone status assignment, but the field is still in great need of an agreed-upon data collection method.

With this broadened view of the keystone species concept, keystone ecology can readily adapt to an applied context. This includes acknowledging that the species that are more likely to receive conservation funding are not always species that elicit the greatest community response (Davidson et al. 2012, Albert et al. 2018, Donkersley et al. 2022). Our findings provide an extensive view on keystone diversity, as well as keystone vulnerability in relation to human disturbance. Together, these perspectives contribute to a growing pool of community ecology knowledge, which will be vital in mitigating future threats against keystones.

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Appendix A: Methods and Results

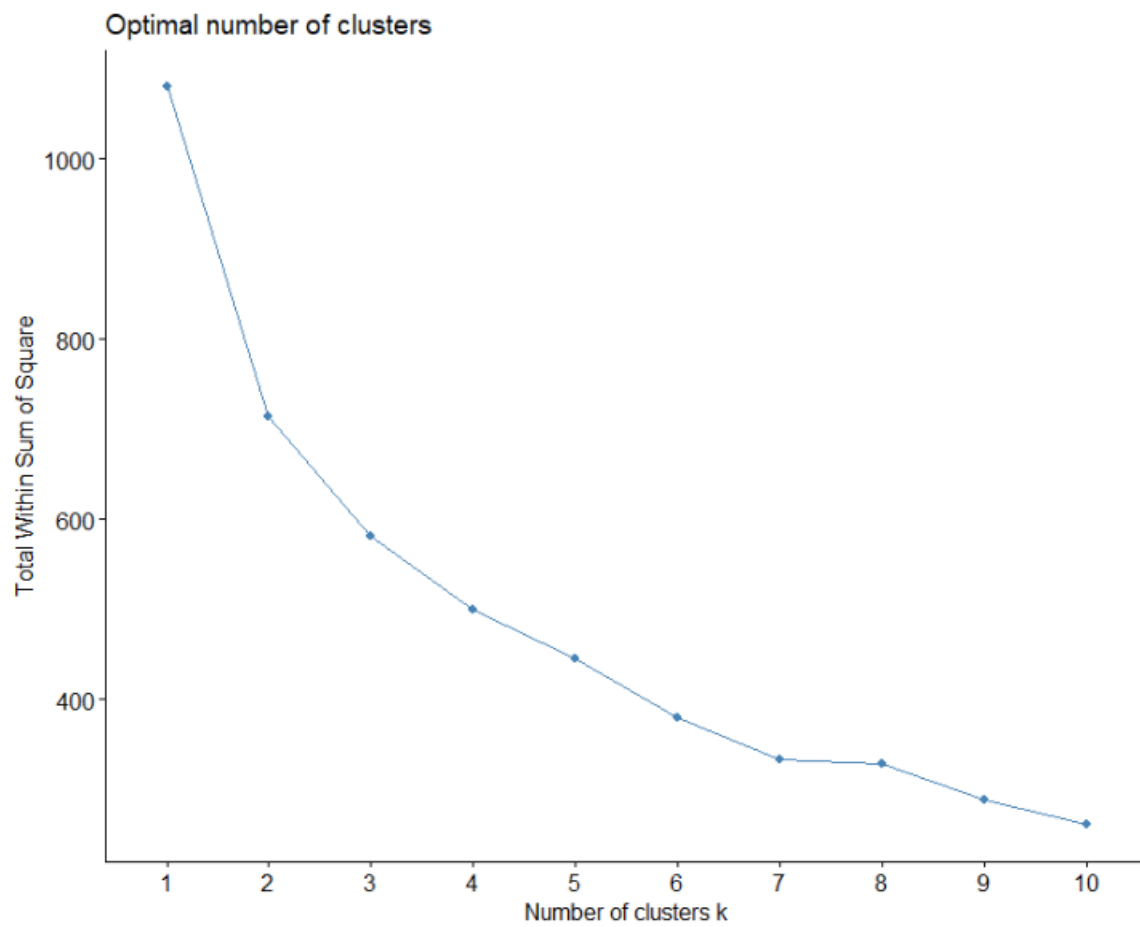


Figure S1. An elbow graph for the k-means clustering analysis validation, indicating the optimal number of clusters (k=5).

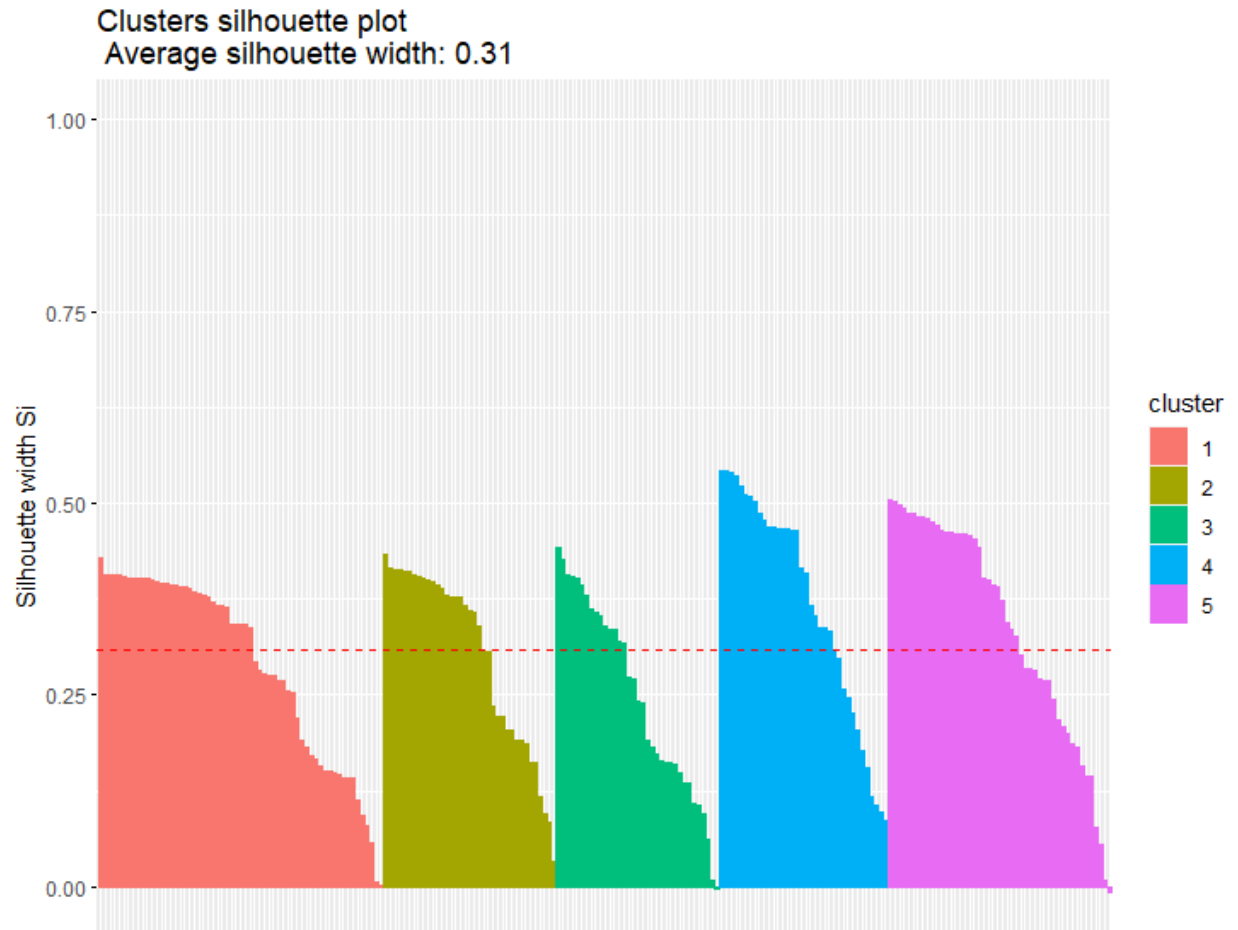


Figure S2. Clustering validation performed to assess the clustering performance of $k = 5$ clusters.

A silhouette with of 0.31 indicates a fair clustering performance.

Calculating sampling variance of effect sizes

We calculated the sampling variance for each species with the odds ratio:

$$\text{Variance (RR)} = (1/O_{\text{Absent}}) + (1/O_{\text{Present}})$$

where O_{Absent} = the number of observations in keystone extirpated or declined systems and O_{Present} = the number of observations in the keystone present or high-density scenario. We generally considered each site (i.e., study location) as an independent observation. In cases of one study site but multiple similar species in the community response measure (e.g., three *Daphnia spp.* responding to a keystone's absence), each species' community response was considered an observation.

Assessing publication bias

We took several different strategies to address potential bias. When searching for literature, we included gray literature (such as theses; $n = 5$ cases), or papers in a variety of languages (as detected by our search engines; $n = 3$). We reason that including these countered any potential publication bias towards studies with larger magnitudes of community responses that are more likely to survive editorial- and peer-reviewed.

To further address any possible publication bias or small sample size, we used funnel plots, which mapped the residuals from RR against the standard error (Figure S3). We then ran an Egger's test to measure the asymmetry of the plot; these tests did not reveal any correlation between the response ratio and the size of the sampling variances ($z = -0.820$, $p = 0.41$), suggesting no evidence of publication bias.

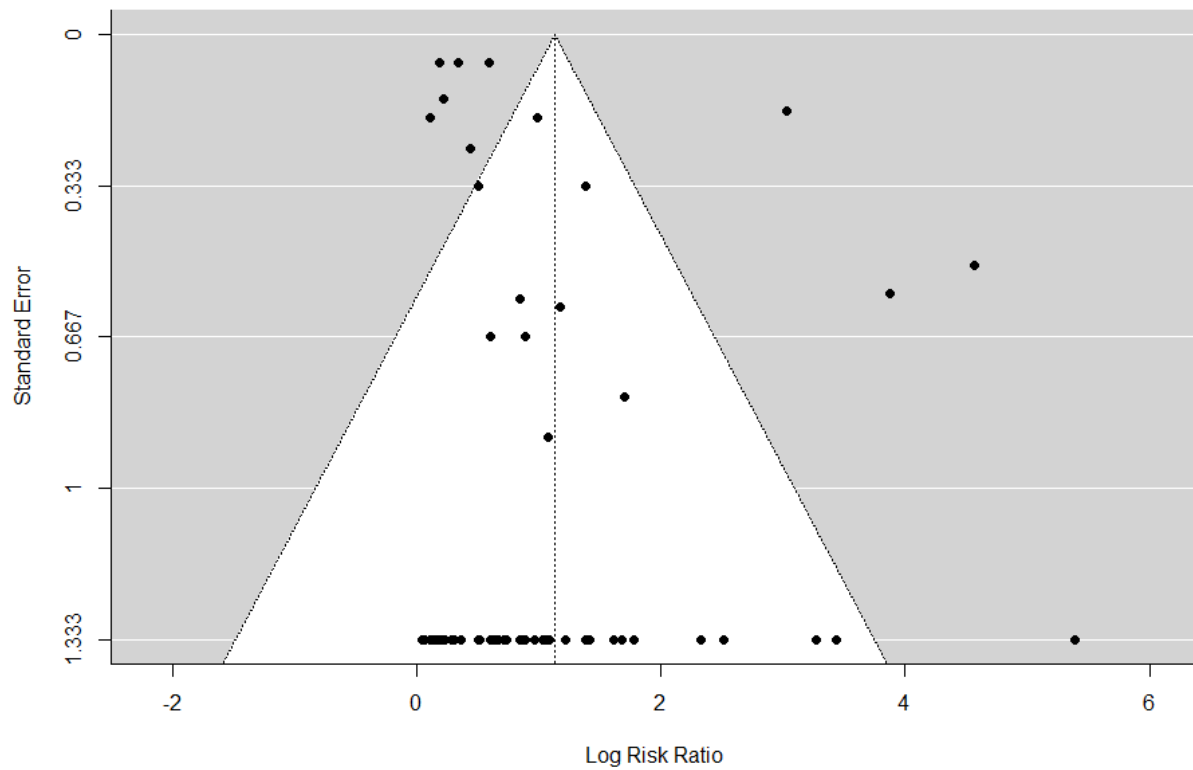


Figure S3. Funnel plot depicting the relationship between community response (Response Ratio), and standard error.

Table S1. Disturbance context, role, trophic level, and body mass multimodal model set with rankings.

Predictors	AICc	Δ AIC	Weight
Community response ~ Disturbance context + Keystone role + Trophic level + Body mass	236.2	0.00	0.644
Community response ~ Disturbance context + Keystone role + Trophic level + Body mass + Trophic level*Body mass	239.5	3.37	0.136
Community response ~ Disturbance context + Keystone role + Trophic level + Body mass + Trophic level*Body mass + Keystone role*Body mass	240.61	4.41	0.081
Community response ~ Disturbance context + Keystone role + Trophic level + Body mass + Trophic level*Keystone role + Trophic level*Body mass + Keystone role*Body mass	241.57	5.38	0.050
Community response ~ Disturbance context + Keystone role + Trophic level + Body mass + Trophic level*Keystone role + Trophic level*Body mass + Keystone role*Body mass + Disturbance context*Keystone role + Disturbance context*Trophic level + Disturbance context*Body mass	247.50	11.30	0.003

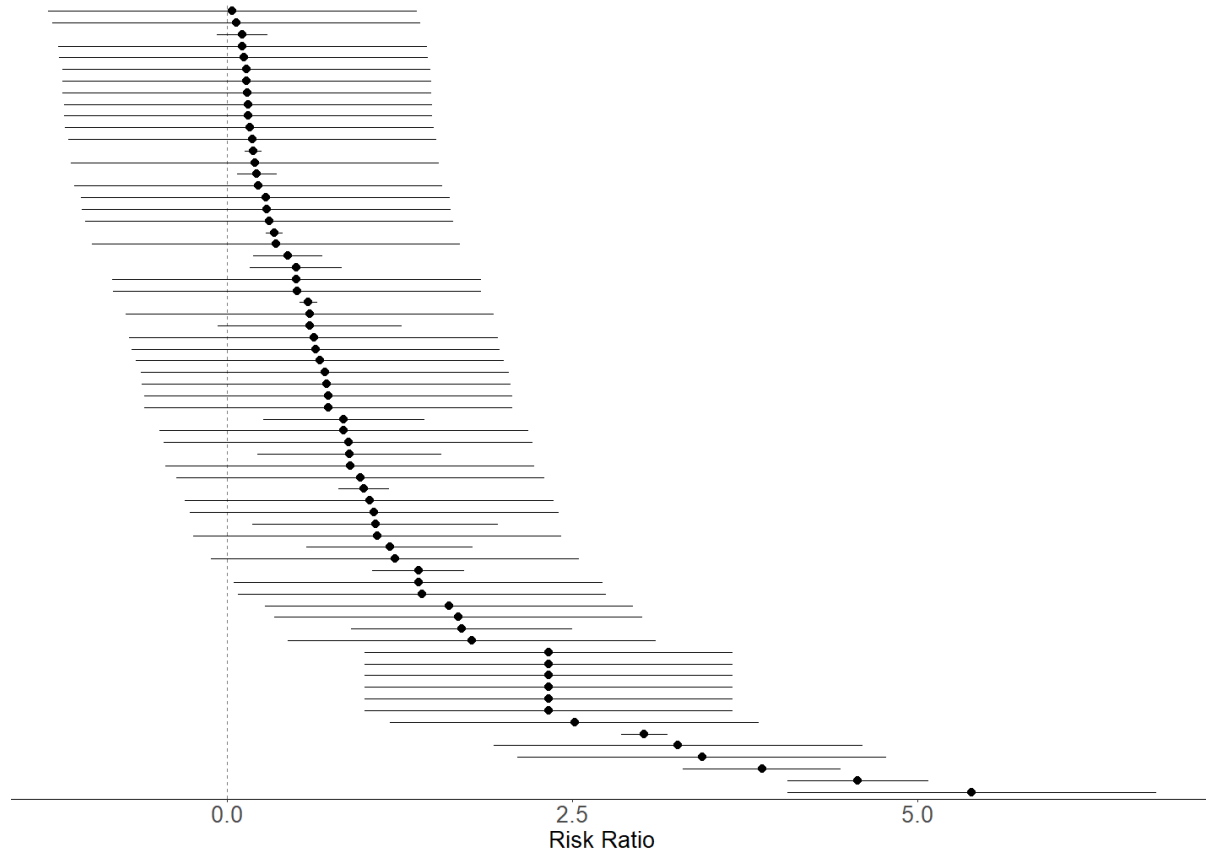
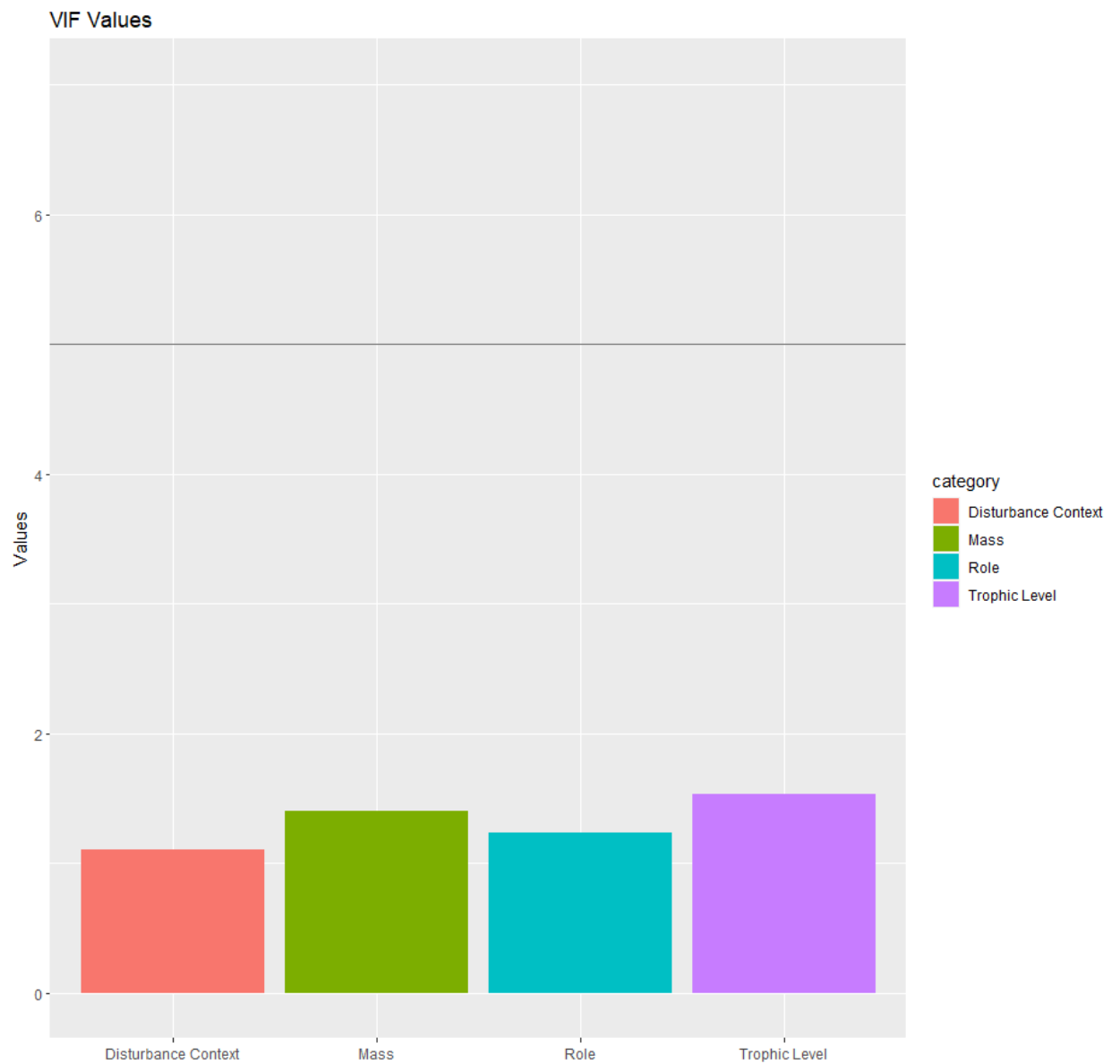


Figure S4. Community response elicited by keystone extirpation or decline displayed for each case study ($n = 111$ effect sizes, ordered from low to high). The change in community response to keystone loss was used to calculate the effect size standardized as a Response Ratio (RR) for the meta-analysis, where $RR = \ln(X_A/X_B)$.

Figure S5. A VIF graph for each predictor used in the community response multi-modal set. The black line ($y = 5$) indicates the threshold for collinearity .



Appendix B: Database: Animals Identified as Keystones

Table S2.

Descriptions of the animals identified as keystone species included in our study, along with the citation, taxonomic Order, community response, and authors' justification for keystone status.

Latin name	Common name	Order	Title	Authors	Year	Journal	Community response	Additional community response	Justification for keystone status	Detailed justification
<i>Acanthaster cf. solaris</i>	Crown-of-Thorns-seastar	Valvatida	Larval cloning in the crown-of-thorns sea star, a keystone coral predator	Allen et al.	2019	Marine Ecology Progress Series	Abundance	Biodiversity	Post-hoc	Determined from literature assessment
<i>Alligator mississippiensis</i>	American Alligator	Crocodylia	Effect of Red Imported Fire Ant Envenomization on Neonatal American Alligators	Allen et al.	1999	Journal of Herpetology	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
<i>Alosa pseudoharengus</i>	Alewife	Clupeiformes	Intraspecific variation in a predator affects community structure and cascading trophic interactions	Post et al.	2008	Ecology	Life history	No secondary response	Post-hoc	Determined from literature assessment
<i>Alpheus japonicus</i>	Japanese Snapping Shrimp	Decapoda	Using network analysis to identify keystone species in the food web of Haizhou Bay, China	Wu et al.	2019	Marine and Freshwater Research	Abundance	No secondary response	Primary	network
<i>Ambystoma talpoideum</i>	Mole Salamander	Urodela	Identifying potential keystone species from field data – an example	Fauth	2002	Ecology Letters	Biodiversity	No secondary response	Primary	Empirical observation or experiment

			from temporary ponds							
<i>Ammodytes tobianus</i>	Lesser Sand Eel	Trachiniformes	Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea	Furness and Tasker	2000	Marine Ecology	Life history	No secondary response	Primary	Empirical observation or experiment
Ammodytidae	Sand Lace	Trachiniformes	Report on identification of keystone species and processes across regional seas	Frederiksen et al.	2006	Journal of Animal Ecology	Life history	No secondary response	Post-hoc	Determined from literature assessment
<i>Anax junius</i>	Common Green Darner	Odonata	Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem	Rudolf and Rasmussen	2013	Ecology	Abundance	No secondary response	Primary	Empirical observation or experiment
<i>Anser caerulescens</i>	Snow goose	Anseriformes	Destruction of Wetland Habitats by Lesser Snow Geese: A Keystone Species on the West Coast of Hudson Bay	Kerbes et al.	1990	Journal of Applied Ecology	Biodiversity	No secondary response	Primary	Empirical observation or experiment
<i>Aphaenogaster rudis</i>	Funnel Ant	Hymenoptera	Forest invader replaces predation but not dispersal services by a keystone species	Warren et al.	2015	Biological Invasions	Abundance	No secondary response	Primary	Empirical observation or experiment
<i>Apis mellifera</i>	Western Honey Bee	Hymenoptera	Plant survival and keystone pollinator species in stochastic coextinction models: role of intrinsic	Traveset et al.	2017	Scientific Reports	Life history	No secondary response	Primary	network

			dependence on animal-pollination							
<i>Arbacia lixula</i>	Black Sea Urchin	Arbacioida	Enjoying the warming Mediterranean: Transcriptomic responses to temperature changes of a thermophilous keystone species in benthic communities	Pérez-Portela et al.	2020	Molecular Ecology	Abundance	No secondary response	Post-hoc	Determined from literature assessment
<i>Arenicola marina</i>	Lugworm	Patellogastropoda	Ecosystem engineering in intertidal sand by the lugworm <i>Arenicola marina</i>	Volkenborn	2006	PhD Thesis, University of Bremen	Chemical and Energy Cycling	No secondary response	Post-hoc	Determined from literature assessment
<i>Astacus astacus</i>	Noble Crayfish	Decapoda	Native and alien crayfish species: do their trophic roles differ?	Weinländer and Füreder	2016	Freshwater Science	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
<i>Asterias rubens</i>	Common Starfish	Forcipulatida	The stars are out: Predicting the effect of seawater freshening on the ecological impact of a sea star keystone predator	Dickey et al.	2021	Ecological Indicators	Abundance	No secondary response	Post-hoc	Determined from literature assessment
<i>Austropotamobius torrentium</i>	Stone Crayfish	Decapoda	Native and alien crayfish species: do their trophic roles differ?	Weinländer and Füreder	2016	Freshwater Science	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
<i>Azteca sericeasur</i>	Arboreal Nesting Ants	Hymenoptera	A Keystone Ant Species Provides Robust Biological Control of the Coffee Berry Borer Under Varying Pest Densities	Morris et al.	2015	PLOS ONE	Abundance	Biodiversity	Post-hoc	Determined from literature assessment
<i>Balaenoptera acutorostrata</i>	Minke Whale	Cetartiodactyla	Existing biodiversity, non-indigenous species, food-web and seafloor integrity GEnS	Teixeira et al.	2014	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment

			indicators. DEVOTES FP7 Project							
Balaenoptera musculus	Blue Whale	Cetartiodactyla	Southern Ocean iron fertilization by baleen whales and Antarctic krill	Nicol et al.	2010	Fish and Fisheries	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
Balaenoptera musculus breviceuda	Pygmy Whale	Cetartiodactyla	Southern Ocean iron fertilization by baleen whales and Antarctic krill	Nicol et al.	2010	Fish and Fisheries	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
Balaenoptera physalus	Fin Whale	Cetartiodactyla	Southern Ocean iron fertilization by baleen whales and Antarctic krill	Nicol et al.	2010	Fish and Fisheries	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
Balistapus undulatus	Red-lined triggerfish	Tetraodontiformes	Recovery of a coral reef keystone predator, Balistapus undulatus, in East African marine parks	McClanahan	2000	Biological Conservation	Abundance	No secondary response	Primary	Empirical observation or experiment
Bettongia lesueur	Burrowing bettong	Rodentia	Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape	James and Eldridge	2007	Biological Conservation	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
Bison bonasus	European bison	Cetartiodactyla	Influence of management practices on large herbivore diet— Case of European bison in Białowieża Primeval Forest (Poland)	Kowalczyk et al.	2010	Forest Ecology and Management	Abundance	No secondary response	Primary	Empirical observation or experiment
Boreogadus saida	Polar Cod	Gadiformes	Shipping alters the movement and behavior of Arctic cod (Boreogadus saida), a keystone fish in Arctic marine ecosystems	Ivanova et al.	2020	Ecological Applications	Abundance	No secondary response	Post-hoc	Determined from literature assessment

Branchinecta orientalis	Fairy Shrimp	Decapoda	The keystone role of anostracans and copepods in European soda pans during the spring migration of waterbirds	Horváth et al.	2013	Freshwater Biology	Biodiversity	No secondary response	Primary	Empirical observation or experiment
Callianassa filholi	Ghost Shrimp	Decapoda	Temporal and spatial variation in macrofauna community composition imposed by ghost shrimp Callianassa filholi bioturbation	Berkenbusch et al. 2000	2000	Marine Ecology Progress Series	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
Canis lupus	Gray Wolf	Carnivora	Trophic cascades linking wolves (Canis lupus), coyotes (Canis latrans), and small mammals	Miller et al.	2012	Canadian Journal of Zoology	Abundance	Behavioral	Primary	Empirical observation or experiment
Canis lupus dingo	Dingo	Carnivora	Keystone effects of an alien top-predator stem extinctions of native mammals	Letnic et al.	2009	Proceedings of the Royal Society B: Biological Sciences	Abundance	No secondary response	Primary	Empirical observation or experiment
Carcharhinus leucas	Bull Shark	Carcharhiniformes	Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean	Myers et al.	2007	Science	Abundance	No secondary response	Post-hoc	meta-analysis
Carcharhinus limbatus	Blacktip Shark	Carcharhiniformes	Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean	Myers et al.	2007	Science	Abundance	No secondary response	Post-hoc	meta-analysis
Carcharhinus obscurus	Dusky Shark	Carcharhiniformes	Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean	Myers et al.	2007	Science	Abundance	No secondary response	Post-hoc	meta-analysis
Carcharhinus plumbeus	Sandbar Shark	Carcharhiniformes	Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean	Myers et al.	2007	Science	Abundance	No secondary response	Post-hoc	meta-analysis

<i>Caretta caretta</i>	Loggerhead Sea Turtle	Testudines	Existing biodiversity, non-indigenous species, food-web and seafloor integrity GEnS indicators. DEVOTES FP7 Project	Teixeira et al.	2014	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
<i>Carollia perspicillata</i>	Seba's short tailed bat	Chiroptera	Keystone species in seed dispersal networks are mainly determined by dietary specialization	Mello et al.	2015	Oikos	Abundance	No secondary response	Primary	network
<i>Castor canadensis</i>	North American beaver	Rodentia	Trends in Rocky Mountain amphibians and the role of beaver as a keystone species	Hossack et al.	2015	Biological Conservation	Abundance	Physical Effects	Primary	Empirical observation or experiment
<i>Castor fiber</i>	Eurasian Beaver	Rodentia	Are beavers a solution to the freshwater biodiversity crisis?	Law et al.	2019	Diversity and Distributions	Biodiversity	Physical Effects	Primary	Empirical observation or experiment
<i>Casuarius bennetti</i>	Dwarf Cassowary	Casuariiformes	The Frugivore Community and the Fruiting Plant Flora in a New Guinea Rainforest: Identifying Keystone Frugivores	Mack and Wright	2005	Tropical Fruits and Frugivores	Biodiversity	No secondary response	Primary	network
<i>Centrophorus granulosus</i>	Gulper shark	Squaliformes	The keystone species in the demersal community from the santa maria di leuca cold-water province (mediterranean sea)	Carlucci et al.	2013	Biologia marina mediterranea	Abundance	No secondary response	Primary	network
<i>Cerastoderma edule</i>	Common Cockle	Cardiida	Co-occurrence of pathogen assemblages in a keystone species the common	Albuixech-Martí et al.	2021	Parasitology	Chemical and Energy Cycling	No secondary response	Post-hoc	Determined from literature assessment

			cockle Cerastoderma edule on the Irish coast							
Ceratogymna atrata	Black-casqued Hornbill	Bucerotiformes	Habitat use and resource tracking by African Ceratogymna hornbills: implications for seed dispersal and forest conservation	Whitney and Smith	1998	Animal Conservation	Abundance	Biodiversity	Primary	Empirical observation or experiment
Ceratogymna cylindricus albotibialis	Brown-cheeked Hornbill	Bucerotiformes	Habitat use and resource tracking by African Ceratogymna hornbills: implications for seed dispersal and forest conservation	Whitney and Smith	1998	Animal Conservation	Abundance	Biodiversity	Primary	Empirical observation or experiment
Chaetodipus baileyi	Bailey's Pocket Mouse	Rodentia	Delayed Compensation for Missing Keystone Species by Colonization	Ernest and brown	2001	Science	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
Chamelea gallina	Striped Venus	Venerida	Bulgarian Initial assessment and GES Report.	BSBD	2013	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Clupea harengus	Atlantic Herring	Clupeiformes	Human-induced Trophic Cascades and Ecological Regime Shifts in the Baltic Sea	Österblom et al.	2007	Ecosystems	Biodiversity	Chemical and Energy Cycling	Post-hoc	Determined from literature assessment
Colaptes auratus	Yellow-shafted Flicker	Piciformes	Nest sites and nest webs for cavity-nesting communities in interior british columbia, canada: nest characteristics and niche partitioning	Martin et al.	2004	The Condor	Physical Effects	No secondary response	Primary	Empirical observation or experiment
Concholepas concholepas	Chilean abalone	Neogastropoda	Coastal marine communities: trends and perspectives from	Castilla	1999	Trends in Ecology & Evolution	Abundance	No secondary response	Post-hoc	Determined from literature assessment

			human-exclusion experiments							
Connochaetes taurinus	Wildebeest	Artiodactyla	Mammal population regulation, keystone processes and ecosystem dynamics.	Sinclair	2003	Philosophical Transactions of the Royal Society B: Biological Sciences	Abundance	Physical Effects	Primary	network
Cornitermes cumulans	Kollar termite	Blattodea	The Termitaria of Cornitermes cumulans (Isoptera, Termitidae) and Their Role in Determining a Potential Keystone Species	Redford	1984	Biotropica	Biodiversity	No secondary response	Primary	Empirical observation or experiment
Cottus gobio	European Bullhead	Scorpaeniformes	Trophic trickles and cascades in a complex food web: impacts of a keystone predator on stream community structure and ecosystem processes	Woodward et al.	2008	Oikos	Abundance	Chemical and Energy Cycling	Primary	Empirical observation or experiment
Crangon crangon	Brown shrimp	Decapoda	Ecological perspectives of The north sea c. Crangon fishery	Doeksen	2006	BSc Thesis, Wageningen University	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Crocodylus niloticus	Nile crocodile	Crocodylia	Conservation and management of crocodiles in Africa	A.C. Pooley	1973	Journal of the South African Wildlife Management Association	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
Culter alburnus	Topmouth Cutler	Cypriniformes	Using a topological approach to identify keystone species of fish in eutrophic lake ecosystems: A	Ren et al.	2022	Fisheries Management and Ecology	Abundance	No secondary response	Primary	network

			case of Zhushan Bay, Taihu Lake							
Culter mongolicus	Mongolian Redfin	Cypriniformes	Using a topological approach to identify keystone species of fish in eutrophic lake ecosystems: A case of Zhushan Bay, Taihu Lake	Ren et al.	2022	Fisheries Management and Ecology	Abundance	No secondary response	Primary	network
Cynomys gunnisoni	Gunnison's Prairie Dog	Rodentia	Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands	Davidson et al.	2013	Frontiers in Ecology and the Environment	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
Cynomys ludovicianus	Black-tailed Prairie Dog	Rodentia	Direct and indirect effects of a keystone engineer on a shrubland-prairie food web	Duchardt. Et al	2021	Ecology	Biodiversity	Physical Effects	Primary	Empirical observation or experiment
Daphnia galeata	Daphnia spp.	Anomopoda	Daphnia as keystone predators: effects on phytoplankton diversity and grazing resistance	Sarnelle	2005	Journal of Plankton Research	Biodiversity	No secondary response	Primary	Empirical observation or experiment
Daphnia magna	Daphnia spp.	Anomopoda	Daphnia as keystone predators: effects on phytoplankton diversity and grazing resistance	Sarnelle	2005	Journal of Plankton Research	Biodiversity	No secondary response	Primary	Empirical observation or experiment
Dascyllus trimaculatus	Three Spotted Damselfish	Perciformes	The Role of threespot damselfish as a keystone species in a bahamian patch reef	Axline-Minotti	2003	Msc. Diss. Ohio State University	Behavioral	Biodiversity	Primary	Empirical observation or experiment
Delphinus delphis	Common Dolphin	Cetartiodactyla	Overfishing of top predators eroded the resilience of the Black Sea system regardless of the climate and	Llope et al.	2011	Global Change Biology	Abundance	Chemical and Energy Cycling	Post-hoc	Determined from literature assessment

			anthropogenic conditions							
<i>Delphinus delphis ponticus</i>	Black Sea Common Dolphin	Cetartiodactyla	Overfishing of top predators eroded the resilience of the Black Sea system regardless of the climate and anthropogenic conditions	Llope et al.	2011	Global Change Biology	Abundance	Chemical and Energy Cycling	Post-hoc	Determined from literature assessment
<i>Diadema africanum</i>	Long-spined Sea Urchin	Diadematoidea	Before and after a disease outbreak: Tracking a keystone species recovery from a mass mortality event	Gizzi et al.	2020	Marine Environmental Research	Abundance	No secondary response	Post-hoc	Determined from literature assessment
<i>Diplodus puntazzo</i>	Sheepshead Bream	Perciformes	Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea	Coll and Libralato	2012	Fish and Fisheries	Abundance	Chemical and Energy Cycling	Primary	network
<i>Dipodomys ingens</i>	Giant Kangaroo Rat	Rodentia	Evaluating current and future range limits of an endangered, keystone rodent (<i>Dipodomys ingens</i>)	Widick and Bean	2019	Diversity and Distributions	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
<i>Dipodomys merriami</i>	Merriam's Kangaroo Rat	Rodentia	Control of a Desert-Grassland Transition by a Keystone Rodent Guild	Brown and Heske	1990	Science	Abundance	Chemical and Energy Cycling	Primary	Empirical observation or experiment
<i>Dipodomys ordii</i>	Ord's Kangaroo Rat	Rodentia	Control of a Desert-Grassland Transition by a Keystone Rodent Guild	Brown and Heske	1990	Science	Abundance	Chemical and Energy Cycling	Primary	Empirical observation or experiment
<i>Dipodomys spectabilis</i>	Banner-tailed kangaroo rat	Rodentia	Presence/absence of a keystone species as an indicator of rangeland health	Krogh et al	2002	Journal of Arid Environments	Abundance	Chemical and Energy Cycling	Primary	Empirical observation or experiment

Dipodomys stephensi	Stephen's Kangaroo Rat	Rodentia	Keystone effects of the endangered Stephens' kangaroo rat (Dipodomys stephensi)	Brock and Kelt	2004	Biological Conservation	Abundance	Biodiversity	Primary	Empirical observation or experiment
Dobsonia magna	Flying Fox	Chiroptera	The Frugivore Community and the Fruiting Plant Flora in a New Guinea Rainforest: Identifying Keystone Frugivores	Mack and Wright	2005	Tropical Fruits and Frugivores	Abundance	No secondary response	Primary	network
Dolichotis patagonum	Patagonian Mara	Rodentia	Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands	Davidson et al.	2012	Frontiers in Ecology and the Environment	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
Donacilla cornea	Donacilla cornea		Bulgarian Initial assessment and GES Report.	BSBD	2013	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Donax trunculus	Abrupt wedge shell	Cardiida	Bulgarian Initial assessment and GES Report.	BSBD	2013	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Dromiciops gliroides	Monito del Monte	Microbiotheria	The disruption of a keystone interaction erodes pollination and seed dispersal networks	Vitali et al.	2022	Ecology	Biodiversity	No secondary response	Primary	network
Dryocopus martius	Black woodpecker	Piciformes	Modelling distribution and potential overlap between Boreal Owl Aegolius funereus and Black Woodpecker Dryocopus martius: implications for management and monitoring plans	Brambilla et al.	2013	Bird Conservation International	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment

Ducula zoeae	Fruit Pigeon	Columbiformes	The Frugivore Community and the Fruiting Plant Flora in a New Guinea Rainforest: Identifying Keystone Frugivores	Mack and Wright	2005	Tropical Fruits and Frugivores	Abundance	No secondary response	Primary	network
Echinus esculentus	Edible sea urchin	Camarodonta	Sea urchin grazing and kelp re-vegetation in the NE Atlantic	Norderhaug and Christie	2009	Marine Biology Research	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Eciton burchelli	Army Ant	Hymenoptera	Habitat fragmentation, percolation theory and the conservation of a keystone species	Boswell et al.	1998	Proceedings of the Royal Society of London. Series B: Biological Sciences	Biodiversity	Physical Effects	Primary	network
Engraulis encrasicolus	European Anchovy	Clupeiformes	Overfishing drives a trophic cascade in the Black Sea	Daskalov	2022	Marine Ecology Progress Series	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Enhydra lutris	Sea Otter	Carnivora	Limited effects of a keystone species: trends of sea otters and kelp forests at the Semichi Islands, Alaska	Konar	2000	Marine Ecology Progress Series	Abundance	Life History	Primary	Empirical observation or experiment
Epinephelus marginatus	Dusky Grouper	Perciformes	Rapid Decline of Nassau Grouper Spawning Aggregations in Belize: Fishery Management and Conservation Needs	Sala et al.	2001	Fisheries	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Eschrichtius robustus	Gray Whale	Cetartiodactyla	Destruction and Opportunity on the Sea Floor: Effects of Gray Whale Feeding	Oliver and Slattery	1985	Ecology	Biodiversity	Physical Effects	Primary	Empirical observation or experiment
Esox lucius	Northern Pike	Esociformes	Salmonid or nonsalmonid lakes: predicting the fate of northern	Spens and Ball	2008	Canadian Journal of Fisheries	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment

			boreal fish communities with hierarchical filters relating to a keystone piscivore			and Aquatic Sciences				
<i>Euastacas armatus</i>	Murray Crayfish	Decapoda	It's not there, but it could be: a renewed case for reintroduction of a keystone species into the Lower River Murray	Whiterod and Zukowski	2019	Transactions of the Royal Society of South Australia	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
<i>Euhrychiopsis lecontei</i>	Weevil	Coleoptera	Is There a New Keystone Species in North American Lakes and Rivers?	Creed	2000	Oikos	Abundance	No secondary response	Post-hoc	Determined from literature assessment
<i>Eupomacentrus planifrons</i>	Threespot Damselfish	Perciformes	The Threespot Damselfish: A noncarnivorous keystone species	Williams	1990	The American Naturalist	Behavioral	Biodiversity	Post-hoc	Determined from literature assessment
<i>Eurosta solidaginis</i>	Goldenrod gall Fly	Diptera	Keystone Individuals Alter Ecological and Evolutionary Consumer-Resource Dynamics	Start	2018	The American Naturalist	Life history	No secondary response	Primary	Empirical observation or experiment
<i>Faxonius rusticus</i>	Rusty Crayfish	Decapoda	How a trematode parasite (<i>Microphallus Ward, 1901</i>) impacts the grazing behavior of an aquatic keystone species, the rusty crayfish <i>Faxonius rusticus</i> Girard, 1852 (Decapoda: Decapoda: Astacidea: Cambaridae)	MacKay and Moore	2021	Journal of Crustacean Biology	Abundance	No secondary response	Post-hoc	Determined from literature assessment
<i>Formica rufa</i>	Red Wood Ant	Hymenoptera	The distribution of a group of keystone species is not associated with	Fitzpatrick et al.	2021	Diversity and Distributions	Abundance	Biodiversity	Primary	network

			anthropogenic habitat disturbance							
Gadus morhua	Atlantic Cod	Gadiformes	Meta-Analysis of Cod-Shrimp Interactions Reveals Top-down Control in Oceanic Food Webs	Worm and Meyers	2003	Ecology	Abundance	No secondary response	Post-hoc	meta-anlsysis
Galeocerdo cuvier	Tiger Shark	Carcharhiniiformes	Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade?	Burkholder et al	2012	Journal of Animal Ecology	Behavioral	Life History	Primary	Empirical observation or experiment
Galeus melastomus	Blackmouth Catshark	Carcharhiniiformes	The keystone species in the demersal community from the santa maria di leuca cold-water province (mediterranean sea)	Carlucci et al.	2013	Biologia marina mediterranea	Abundance	No secondary response	Primary	network
Gammarus fossarum	Freshwater Shrimp	Decapoda	Additive effects of temperature and infection with an acanthocephalan parasite on the shredding activity of Gammarus fossarum (Crustacea: Amphipoda): the importance of aggregative behavior	Labaude et al.	2017	Global Change Biology	Chemical and Energy Cycling	No secondary response	Post-hoc	Determined from literature assessment
Gecarcoidea natalis	Christmas Island red crab	Decapoda	Invasional 'meltdown' on an oceanic island	O'Dowd et al.	2003	Ecology Letters	Abundance	Chemical and Energy Cycling	Post-hoc	Determined from literature assessment
Geomys bursarius	Plains Pocket Gopher	Rodentia	Effects of Plains Pocket Gopher (Geomys bursarius) Disturbances on	Rogers et al	2013	The American midland Naturalist	Biodiversity	Physical Effects	Primary	Empirical observation or experiment

			Tallgrass-prairie Plant Community Structure							
<i>Glaucomys sabrinus</i>	Northern Flying Squirrel	Rodentia	Ecology of <i>Glaucomys sabrinus</i> : Habitat, Demography, and Community Relations	Smith et al.	2007	Journal of Mammology	Chemical and Energy Cycling	No secondary response	Post-hoc	meta-analysis
<i>Gopher polyphemus</i>	Gopher tortoise	Testudines	Functional relationships reveal keystone effects of the gopher tortoise on vertebrate diversity in a longleaf pine savanna	Catano and Stout	2015	Biodiversity and Conservation	Biodiversity	Physical Effects	Primary	Empirical observation or experiment
<i>Haematopus moquini</i>	African black oystercatchers	Charadriiformes	Diet of the African black oystercatcher <i>Haematopus moquini</i> on rocky shores: spatial, temporal and sex-related variation	Hockey and Branch	1984	African Zoology	Abundance	No secondary response	Primary	Empirical observation or experiment
<i>Halichoerus grypus</i>	Grey seal	Carnivora	Using sensitivity analysis to identify keystone species and keystone links in size-based food webs	Berg et al.	2011	Oikos	Biodiversity	No secondary response	Primary	network
<i>Hesperoleucus symmetricus</i>	California Roach	Cypriniformes	Floods, Food Chains, and Ecosystem Processes in Rivers	Power	1995	Linking Species and Ecosystems	Abundance	Chemical and Energy Cycling	Post-hoc	Determined from literature assessment
<i>Ips typographus</i>	Spruce Bark Beetle	Coleoptera	The European spruce bark beetle <i>Ips typographus</i> in a national park: from pest to keystone species	Müller et al.	2008	Biodiversity and Conservation	Abundance	Biodiversity	Primary	Empirical observation or experiment
<i>Jasus edwardsii</i>	Southern Rock Lobster	Decapoda	Lobsters as keystone: Only in unfished ecosystems?	Eddy et al.	2014	Ecological Modelling	Chemical and Energy Cycling	No secondary response	Primary	network

Lagostomus maximus	Plains Vizcacha	Lagomorpha	Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands	Davidson et al.	2012	Frontiers in Ecology and the Environment	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
Larimichthys polyactis	Redlip Croaker	Acanthuriformes	Using network analysis to identify keystone species in the food web of Haizhou Bay, China	Wu et al.	2019	Marine and Freshwater Research	Abundance	No secondary response	Primary	network
Larus audouinii	Audouin's Gull	Charadriiformes	Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea	Coll and Libralato	2012	Fish and Fisheries	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Lasiorchinus latifrons	Southern hairy-nosed wombat	Diprotodontia	Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands	Davidson et al.	2012	Frontiers in Ecology and the Environment	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
Laternula elliptica	Saltwater Clam	Heterodonta	Anatomy and behavior of Laternula elliptica, a keystone species of the Antarctic benthos (Bivalvia: Anomalodesmata: Laternulidae)	Passos et al.	2022	PeerJ	Chemical and Energy Cycling	No secondary response	Post-hoc	Determined from literature assessment
Leander modestus	Chinese white prawn	Decapoda	Selection of keystone species based on stable carbon and nitrogen isotopes to construct a typical food web on the shore of Xingkai Lake, China	Xing et al.	2021	Ecological Indicators	Abundance	No secondary response	Primary	network

Lentidium mediterraneum	Lentidium mediterraneum	Myida	Bulgarian Initial assessment and GES Report.	BSBD	2013	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Leptochela gracilis	Lesser Glass Shrimp	Decapoda	Using network analysis to identify keystone species in the food web of Haizhou Bay, China	Wu et al.	2019	Marine and Freshwater Research	Abundance	No secondary response	Primary	network
Leptuca leptodactyla	Thin-fingered fiddler crab	Decapoda	Mangrove crabs as ecosystem engineers; with emphasis on sediment processes	Kristensen	2008	Mangrove Macrobenh os Special Issue	Chemical and Energy Cycling	Physical Effects	Primary	Empirical observation or experiment
Leptuca uruguayensis	Uruguayan fiddler crab	Decapoda	Mangrove crabs as ecosystem engineers; with emphasis on sediment processes	Kristensen	2008	Mangrove Macrobenh os Special Issue	Chemical and Energy Cycling	Physical Effects	Primary	Empirical observation or experiment
Lepus americanus	Snowshoe hare	Lagomorpha	Prey availability and ambient temperature influence carrion persistence in the boreal forest	Peers et al.	2020	Journal of Animal Ecology	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
Limaria hians	Gaping file shell	Limida	Limaria hians (Mollusca: Limacea): a neglected reef-forming keystone species	Hall-Spencer and Moore	2000	Aquatic Conservation: Marine and Freshwater Ecosystems	Physical Effects	Biodiversity	Post-hoc	Determined from literature assessment
Loligo plei	Tropical Arrow squid	Myopsida	The trophic role of the squid Loligo plei as a keystone species in the South Brazil Bight ecosystem	Gasalla et al.	2010	ICES Journal of Marine Science	Abundance	No secondary response	Primary	network
Lophius budegassa	Blackbellied Angler	Lophiiformes	The keystone species in the demersal community from the santa maria di leuca cold-water province (mediterranean sea)	Carlucci et al.	2013	Biologia marina mediterranea	Abundance	No secondary response	Primary	network

Loxodonta africana	African elephant	Proboscidea	Elephants and Fire as Causes of Multiple Stable States in the Serengeti-Mara Woodlands	Dublin	1990	Journal of Animal Ecology	Abundance	Physical Effects	Primary	Empirical observation or experiment
Lynx lynx	Eurasian Lynx	Carnivora	Usability of large carnivore as a keystone species in Eastern Black Sea Region, Turkey	Ucarli	2011	African Journal of Biotechnology	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Lynx pardinus	Iberian lynx	Carnivora	Positive Effects on Game Species of Top Predators by Controlling Smaller Predator Populations: An Example with Lynx, Mongooses, and Rabbits	Palomares et al	1994	Conservation Biology	Abundance	No secondary response	Primary	Empirical observation or experiment
Macoma balthica	Baltic clam	Cardiida	Burrowing behaviour of the Baltic clam Macoma balthica: effects of sediment type, hypoxia and predator presence	Tallqvist	2001	Marine Ecology Progress Series	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
Macrotis lagotis	Greater Bilby	Rodentia	Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape	James and Eldridge	2007	Biological Conservation	Biodiversity	Chemical and Energy Cycling	Primary	Empirical observation or experiment
Margaritifera margaritifera	Freshwater Pearl Mussel	Unionida	Climate Warming as a Possible Trigger of Keystone Mussel Population Decline in Oligotrophic Rivers at the Continental Scale	Bolotov et al.	2018	Scientific Reports	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Marmota himalayana	Himalayan Marmot	Rodentia	Ecological roles and conservation challenges of social, burrowing,	Davidson et al.	2016	Frontiers in Ecology and the	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment

			herbivorous mammals in the world's grasslands			Environment				
<i>Marmota sibirica</i>	Siberian Marmot	Rodentia	Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands	Davidson et al.	2015	Frontiers in Ecology and the Environment	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
<i>Mecistops cataphractus</i>	Slender-snouted crocodile	Crocodylia	Conservation and management of crocodiles in Africa	A.C. Pooley	1973	Journal of the South African Wildlife Management Association	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
<i>Megaptera novaeangliae</i>	Humpback Whale	Cetartiodactyla	Southern Ocean iron fertilization by baleen whales and Antarctic krill	Nicol et al.	2010	Fish and Fisheries	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
<i>Merluccius merluccius</i>	European Hake	Gadiformes	Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea	Coll and Libralato	2012	Fish and Fisheries	Abundance	Chemical and Energy Cycling	Post-hoc	Determined from literature assessment
<i>Meyenaster gelatinosus</i>	Large Spiny Seastar	Forcipulatida	Quantifying keystone species complexes: Ecosystem-based conservation management in the King George Island (Antarctic Peninsula)	Ortiz et al.	2017	Ecological Indicators	Physical Effects	No secondary response	Primary	network
<i>Micropterus punctulatus</i>	Spotted Bass	Perciformes	Grazing Minnows, Piscivorous Bass, and Stream Algae: Dynamics of a Strong Interaction	Power and Gregoire	1978	Ecology	Abundance	No secondary response	Primary	Empirical observation or experiment
<i>Micropterus salmoides</i>	Largemouth Bass	Perciformes	Perturbation and Resilience: A Long-Term, Whole-Lake Study	Mittelbach et al.	1995	Ecology	Abundance	Life History	Primary	Empirical observation or experiment

			of Predator Extinction and Reintroduction							
Microrhopala vittata	Chrysomelid beetle	Coleoptera	Herbivory and Plant Species Coexistence: Community Regulation by an Outbreking Phytophagous Insect	Carson and Root	2000	Ecological Monographs	Abundance	Biodiversity	Primary	Empirical observation or experiment
Modiolula phaseolina	Bean Horse Mussel	Mytilida	Bulgarian Initial assessment and GES Report.	BSBD	2013	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Modiolus modiolus	Horse mussel	Mytilida	Community convergence and recruitment of keystone species as performance indicators of artificial reefs	Fariñas-Franco et al.	2013	Journal of Sea Research	Physical Effects	No secondary response	Primary	Empirical observation or experiment
Monachus monachus	Mediterranean Monk Seal	Carnivora	Overfishing drives a trophic cascade in the Black Sea	Daskalov	2022	Marine Ecology Progress Series	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Myliobatis californica	Bat Ray	Myliobatiformes	Experimental Analyses of Structural Regulation in a Marine Sand Community Exposed to Oceanic Swell	Van Blaricom	1982	Ecological Monographs	Biodiversity	Physical Effects	Primary	Empirical observation or experiment
Mysis diluviana	Opossum Shrimp	Mysida	Hydroclimate mediates effects of a keystone species in a coldwater reservoir	Johnson and Martinez	2012	Lake and Reservoir Management	Abundance	Chemical and Energy Cycling	Primary	Empirical observation or experiment
Mytilaster lineatus	Mytilaster lineatus	Mytilida	Existing biodiversity, non-indigenous species, food-web and seafloor integrity GEnS indicators. DEVOTES FP7 Project	Teixeira et al.	2014	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment

Mytilus edulis	Blue Mussel	Mytilida	Effects of cigarette butts on marine keystone species (<i>Ulva lactuca</i> L. and <i>Mytilus edulis</i> L.) and sediment microphytobenthos	Green et al.	2021	Marine Pollution Bulletin	Abundance	Biodiversity	Post-hoc	Determined from literature assessment
Mytilus galloprovincialis	Mediterranean mussel	Mytilida	Existing biodiversity, non-indigenous species, food-web and seafloor integrity GEnS indicators. DEVOTES FP7 Project	Teixeira et al.	2014	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Mytilus galloprovincialis	Mediterranean Mussel	Mytilida	Bulgarian Initial assessment and GES Report.	BSBD	2013	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Mytilus trossulus	Bay Mussel	Mytilida	Importance of ice algae and pelagic phytoplankton as food sources revealed by fatty acid trophic markers in a keystone species (<i>Mytilus trossulus</i>) from the High Arctic	Thyrring et al.	2017	Marine Ecology Progress Series	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Neotoma albigula	Western White-Throated Woodrat	Rodentia	Pack rats (<i>Neotoma</i> spp.): Keystone ecological engineers?	Whitford and Steinberger	2021	Journal of Arid Environments	Biodiversity	Chemical and Energy Cycling	Primary	Empirical observation or experiment
Neotoma micropus	Southern Plains Woodrat	Rodentia	Pack rats (<i>Neotoma</i> spp.): Keystone ecological engineers?	Whitford and Steinberger	2021	Journal of Arid Environments	Biodiversity	Chemical and Energy Cycling	Primary	Empirical observation or experiment
Nocomis biguttatus	Hornyhead Chub	Cypriniformes	Nesting Ecology and Behavior of Hornyhead Chub <i>Nocomis biguttatus</i> , a Keystone Species	Vives	1990	The American Midland Naturalist	Biodiversity	Physical Effects	Post-hoc	Determined from literature assessment

			in Allequash Creek, Wisconsin							
Notophthalmus viridescens	Eastern Newt	Urodela	Identifying potential keystone species from field data – an example from temporary ponds	Fauth	2002	Ecology Letters	Biodiversity	No secondary response	Primary	Empirical observation or experiment
Ochotona curzoniae	Plateau Pika	Lagomorpha	Keystone status of plateau pikas (Ochotona curzoniae): effect of control on biodiversity of native birds	Lai and Smith	2003	Biodiversity and Conservation	Abundance	Biodiversity	Primary	Empirical observation or experiment
Ochotona princeps	American Pika	Rodentia	Influence of Refuging Consumers (Pikas: Ochotona Princeps) on Subalpine Meadow Vegetation	Huntly	1987	Ecology	Abundance	Biodiversity	Primary	Empirical observation or experiment
Octodon degus	Degu	Rodentia	Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands	Davidson et al.	2012	Frontiers in Ecology and the Environment	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
Odocoileus virginianus	White tailed Deer	Artiodactyla	The White-Tailed Deer: A Keystone Herbivore	Waller and Alverson	1997	Wildlife Society Bulletin	Abundance	Biodiversity	Primary	Empirical observation or experiment
Oedemera flavipes	Oedemera flavipes	Coleoptera	Plant survival and keystone pollinator species in stochastic coextinction models: role of intrinsic dependence on animal-pollination	Traveset et al.	2017	Scientific Reports	Biodiversity	No secondary response	Primary	network
Oncorhynchus nerka	Sockeye Salmon	Salmoniformes	Keystone Interactions: Salmon and Bear in Riparian Forests of Alaska	Helfield and Naiman	2006	Ecosystems	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment

Ophiothrix fragilis	Common Brittlestar	Ophiurida	Near-future level of CO2-driven ocean acidification radically affects larval survival and development in the brittlestar <i>Ophiothrix fragilis</i>	Dupont et al.	2008	Marine Ecology Progress Series	Abundance	Biodiversity	Post-hoc	Determined from literature assessment
Oratosquilla oratoria	Japanese Mantis Shrimp	Stomatopoda	Using network analysis to identify keystone species in the food web of Haizhou Bay, China	Wu et al.	2019	Marine and Freshwater Research	Abundance	No secondary response	Primary	network
Oryctolagus cuniculus	European Rabbit	Lagomorpha	Disease-mediated bottom-up regulation: An emergent virus affects a keystone prey, and alters the dynamics of trophic webs	Monterroso et al.	2016	Scientific Reports	Abundance	No secondary response	Primary	Empirical observation or experiment
Osteolaemus tetraspis	African Dwarf Crocodile	Crocodylia	Conservation and management of crocodiles in Africa	A.C. Pooley	1973	Journal of the South African Wildlife Management Association	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
Ostrea edulis	European oyster	Ostreida	Conservation and restoration of a keystone species: Understanding the settlement preferences of the European oyster (<i>Ostrea edulis</i>)	Rodriguez-Perez et al.	2019	Marine Pollution Bulletin	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
Ostrea edulis	Native oyster	Ostreida	The European oyster (<i>Ostrea edulis</i>) and its epibiotic succession	Smyth and Roberts	2010	Hydrobiologia	Biodiversity	No secondary response	Post-hoc	Determined from literature assessment
Otomys sloggetti	Ice Rat	Rodentia	Does the ice rat <i>Otomys sloggetti robertsi</i> contribute to habitat change in Lesotho?	Mokotjomela et al.	2009	Acta Oecologica	Biodiversity	Chemical and Energy Cycling	Primary	Empirical observation or experiment

Otospermophilus beecheyi	California Ground Squirrel	Rodentia	Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands	Davidson et al.	2012	Frontiers in Ecology and the Environment	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
Pagophilus groenlandicus	Harp Seal	Carnivora	An Ecopath Model for the Norwegian and Barents Sea.	Dommasnes et al.	2001	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Pandalus borealis	Northern Shrimp	Decapoda	DNA metabarcoding reveals the importance of gelatinous zooplankton in the diet of Pandalus borealis, a keystone species in the Arctic	Urban et al.	2022	Molecular Ecology	Chemical and Energy Cycling	No secondary response	Post-hoc	Determined from literature assessment
Panthera onca	Jaguar	Carnivora	Ecological Meltdown in Predator-Free Forest Fragments	Terborgh et al.	2001	Science	Abundance	Biodiversity	Primary	Empirical observation or experiment
Paracentrotus lividus	Purple Sea Urchin	Camarodonta	East is East and West is West: Population genomics and hierarchical analyses reveal genetic structure and adaptation footprints in the keystone species Paracentrotus lividus (Echinoidea)	Carreras et al.	2020	Diversity and Distributions	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Paralonchurus brasiliensis	Banded Croaker	Perciformes	Reproductive strategy and fecundity of the keystone species Paralonchurus brasiliensis (Teleostei, Sciaenidae): an image processing	Costa et al.	2015	Environmental Biology of Fishes	Abundance	No secondary response	Post-hoc	Determined from literature assessment

			techniques application							
Paraneohrops planifrons	Freshwater Crayfish	Decapoda	Koura: a keystone species?	Collier et al.	1997	Stream Ecosystems	Abundance	No secondary response	Primary	Empirical observation or experiment
Parasesarma messa	Maroon Mangrove Crab	Amphionidacea	Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity	Smith et al.	1991	Estuarine, Coastal and Shelf Science	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
Patella aspera	Atlantic Limpet	Patellogastropoda	Growth and reproduction of the north-eastern Atlantic keystone species <i>Patella aspera</i> (Mollusca: Patellogastropoda)	Sousa et al.	2017	Helgoland Marine Research	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
Patella candei	Sun limpet	Patella candei	Community structure and dynamics of the azorean rocky intertidal: exploitation of keystone species	Martins	2008	PhD Thesis, Univ. of Plymouth	Abundance	No secondary response	Primary	Empirical observation or experiment
Patella rustica	High-shore Limpet	Patellogastropoda	Growth and Morphological Trends of the Keystone Species <i>Patella rustica</i> Linnaeus, 1758 (Mollusca: Gastropoda) in a Protected Mediterranean Lagoon	Bensaâd-Bendjedid et al.	2022	Acta Zoologica Bulgarica	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Patella vulgata	Common Limpet	Patellogastropoda	A continental scale evaluation of the role of limpet grazing on rocky shores	Coleman et al.	2006	Oecologia	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Pedetes capensis	Springhare	Rodentia	Ecological roles and conservation challenges of social, burrowing,	Davidson et al.	2012	Frontiers in Ecology and the	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment

			herbivorous mammals in the world's grasslands			Environment				
<i>Perca fluviatilis</i>	European Perch	Perciformes	Fish Predation and Benthic Community Structure: The Role of Omnivory and Habitat Complexity	Diehl	1992	Ecology	Abundance	Life History	Primary	Empirical observation or experiment
<i>Phalacrocorax carbo</i>	Great Cormorant	Suliformes	Food consumption by seabirds in Norwegian waters	Barrett et al.	2002	ICES Journal of Marine Science	Abundance	No secondary response	Primary	network
<i>Phoca vitulina</i>	Harbor Seal	Carnivora	Existing biodiversity, non-indigenous species, food-web and seafloor integrity GEnS indicators. DEVOTES FP7 Project	Teixeira et al.	2014	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
<i>Phocoena phocoena</i>	Harbor Porpoise	Cetartiodactyla	Overfishing drives a trophic cascade in the Black Sea	Daskalov	2002	Marine Ecology Progress Series	Abundance	No secondary response	Post-hoc	Determined from literature assessment
<i>Phocoena phocoena relicta</i>	Black Sea Harbor Porpoise	Cetartiodactyla	Overfishing drives a trophic cascade in the Black Sea	Daskalov	2002	Marine Ecology Progress Series	Abundance	No secondary response	Post-hoc	Determined from literature assessment
<i>Pholas dactylus</i>	Common piddock	Myida	Bulgarian Initial assessment and GES Report.	BSBD	2013	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
<i>Pieris rapae</i>	Cabbage White Butterfly	Lepidoptera	Herbivore-induced plant responses in Brassica oleracea prevail over effects of constitutive resistance and result in enhanced herbivore attack	Poelman and Kessler	2010	Ecological Entomology	Abundance	No secondary response	Primary	Empirical observation or experiment
<i>Pisaster ochraceus</i>	Purple Sea Star	Forcipulatida	The Pisaster-Tegula Interaction: Prey Patches, Predator Food Preference, and	Paine	1969	The American Naturalist	Abundance	Biodiversity	Primary	Empirical observation or experiment

			Intertidal Community Structure							
Pomatomus saltatrix	Bluefish	Perciformes	Overfishing drives a trophic cascade in the Black Sea	Daskalov	2002	Marine Ecology Progress Series	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Pomatoschistus microps	Common Goby	Gobiiformes	An abundant small sized fish as keystone species? The effect of Pomatoschistus microps on food webs and its trophic role in two intertidal benthic communities: A modeling approach	Pockberger et al.	2014	Journal of Sea Research	Abundance	No secondary response	Primary	network
Pristomyrmex pungens Mayr	Japanese Queenless Ant	Hymenoptera	Leaf Volatiles from Two Corydalid Species Lure A Keystone Seed-dispersing Ant and Enhance Seed Retrieval	Zhu and Wang	2018	Sociobiology	Abundance	Biodiversity	Post-hoc	Determined from literature assessment
Procambarus alleni	Everglades Crayfish	Decapoda	The effect of hydroperiod on the growth of the crayfish species Procambarus alleni and Procambarus fallax: Two keystone species in the Florida Everglades	Gardener	2006	MSc Diss. Florida Atlantic University	Abundance	Chemical and Energy Cycling	Post-hoc	Determined from literature assessment
Procambarus fallax	Deceitful Crayfish	Decapoda	The effect of hydroperiod on the growth of the crayfish species Procambarus alleni and Procambarus fallax: Two keystone species in the Florida Everglades	Gardener	2006	MSc Diss. Florida Atlantic University	Abundance	Chemical and Energy Cycling	Post-hoc	Determined from literature assessment

Pterodroma gouldi	Grey-faced Petrel	Procellariiformes	Monitoring burrowing petrel populations: A sampling scheme for the management of an island keystone species	Buxton et al.	2016	The Journal of Wildlife Management	Abundance	Chemical and Energy Cycling	Primary	Empirical observation or experiment
Pteropus dasymallus inopinatus	Orii's flying fox	Chiroptera	The role of Orii's flying-fox (Pteropus dasymallus inopinatus) as a pollinator and a seed disperser on Okinawa-jima Island, the Ryukyu Archipelago, Japan	Nakamoto et al.	2008	Ecological Research	Abundance	No secondary response	Primary	Empirical observation or experiment
Pteropus samoensis	Samoan Flying Fox	Chiroptera	Topological keystone species in ecological interaction networks: Considering link quality and non-trophic effects	Vasas and Jordán	2006	Ecological modeling	Physical Effects	No secondary response	Primary	network
Pteropus tonganus	Pacific Flying Fox	Chiroptera	Flying Foxes as Strong Interactors in South Pacific Island Ecosystems: A Conservation Hypothesis	Cox et al.	1991	Conservation Biology	Abundance	Biodiversity	Post-hoc	Determined from literature assessment
Puma concolor	Puma	Carnivora	Summer predation rates on ungulate prey by a large keystone predator: how many ungulates does a large predator kill?	Laundré	2008	Journal of Zoology	Abundance	No secondary response	Primary	Empirical observation or experiment
Pusa hispida	Ringed Seal	Carnivora	Predictions replaced by facts: a keystone species' behavioural responses to declining arctic sea-ice	Hamilton et al.	2015	Biology Letters	Abundance	No secondary response	Post-hoc	Determined from literature assessment

Python molurus bivittatus	Burmese Python	Squamata	Invasive pythons, not anthropogenic stressors, explain the distribution of a keystone species	Sovie et al.	2016	Biological Invasions	Behavioral	No secondary response	Primary	Empirical observation or experiment
Rapana venosa	Veined rapa whelk	Neogastropoda	Bulgarian Initial assessment and GES Report.	BSBD	2013	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Rhyticeros plicatus	Blyth's Hornbill	Bucerotiformes	The Frugivore Community and the Fruiting Plant Flora in a New Guinea Rainforest: Identifying Keystone Frugivores	Mack and Wright	2005	Tropical Fruits and Frugivores	Physical Effects	No secondary response	Primary	network
Sabellaria spinulosa	Ross worm	Sabellariidae	Sabellariaspinulos a reef: a scoring system for evaluating 'reefiness' in the context of the Habitats Directive	Hendrick and Foster-Smith	2006	Journal of the Marine Biological Association of the United Kingdom	Biodiversity	Physical Effects	Post-hoc	Determined from literature assessment
Salangichthys tangkahkeii	Japanese icefish	Osmeriformes	Using a topological approach to identify keystone species of fish in eutrophic lake ecosystems: A case of Zhushan Bay, Taihu Lake	Ren et al.	2022	Fisheries Management and Ecology	Biodiversity	No secondary response	Primary	network
Salminus brasiliensis	Dourado	Characiformes	Climate change will decrease the range of a keystone fish species in La Plata River Basin, South America	Ruaro et al.	2019	Hydrobiologia	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Salmo gairdneri	Rainbow Trout	Salmoniformes	Effects of Fish in River Food Webs	Power	1990	Science	Abundance	No secondary response	Primary	Empirical observation or experiment
Salmo salar	Atlantic Salmon	Salmoniformes	Existing biodiversity, non-indigenous species, food-web and seafloor	Teixeira et al.	2014	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment

			integrity GEnS indicators. DEVOTES FP7 Project							
Salmo trutta	Brown Trout	Salmoniformes	Existing biodiversity, non-indigenous species, food-web and seafloor integrity GEnS indicators. DEVOTES FP7 Project	Teixeira et al.	2014	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Sander lucioperca	Zander	Perciformes	Existing biodiversity, non-indigenous species, food-web and seafloor integrity GEnS indicators. DEVOTES FP7 Project	Teixeira et al.	2014	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Sarda sarda	Atlantic Bonito	Scombriformes	Overfishing drives a trophic cascade in the Black Sea	Daskalov	2022	Marine Ecology Progress Series	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Scomber scombrus	Atlantic mackerel	Scombriformes	Centennial Decline in the Trophic Level of an Endangered Seabird after Fisheries Decline	Becker and Beissinger	2006	Conservation Biology	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
Scophthalmus maximus	Turbot	Pleuronectiformes	The State-of-Art of the Black Sea Turbot Spawning Population off Crimea (1998-2010)	Giragosov and Khanaychenko	2013	Turkish Journal of Fisheries and Aquatic Sciences	Chemical and Energy Cycling	No secondary response	Post-hoc	Determined from literature assessment
Sephanoides sephaniodes	Green-backed firecrown	Apodiformes	Linking Socioeconomics to Biodiversity in the City: The Case of a Migrant Keystone Bird Species	Villaseñor and Escobar	2022	Frontiers in Ecology and Evolution	Biodiversity	No secondary response	Post-hoc	Determined from literature assessment

Sesarma reticulatum	Marsh Crab	Decapoda	Sea-level rise and the emergence of a keystone grazer alter the geomorphic evolution and ecology of southeast US salt marshes	Crotty et al.	2020	Proceedings of the National Academy of Sciences	Abundance	Chemical and Energy Cycling	Primary	Empirical observation or experiment
Sesarma semperi longicristatum	Australasian mangrove crab	Amphionidacea	Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity	Smith et al.	1991	Estuarine, Coastal and Shelf Science	Chemical and Energy Cycling	No secondary response	Primary	Empirical observation or experiment
Siren intermedia	Lesser Siren	Urodela	Identifying potential keystone species from field data – an example from temporary ponds	Fauth	2002	Ecology Letters	Biodiversity	No secondary response	Primary	Empirical observation or experiment
Solenopsis geminata	Fire ant	Hymenoptera	Effect of a Keystone Predaceous Ant, Solenopsis Geminata, on Arthropods in a Tropical Agroecosystem	Risch and Carroll	1982	Ecology	Abundance	No secondary response	Primary	Empirical observation or experiment
Spermophilus citellus	European Ground Squirrel	Rodentia	Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands	Davidson et al.	2012	Frontiers in Ecology and the Environment	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment
Sphyrapicus nuchalis	Red-naped Sapsucker	Piciformes	Double keystone bird in a keystone species complex.	Daily et al.	1993	PNAS	Physical Effects	Biodiversity	Post-hoc	Determined from literature assessment
Sphyrapicus varius	Yellow-bellied Sapsucker	Piciformes	Early breeders choose differently – Refining measures of habitat quality for the yellow-bellied	Squires and Bunnell	2018	PLOS ONE	Biodiversity	Physical Effects	Post-hoc	Determined from literature assessment

			sapsucker (Sphyrapicus varius), a keystone species in the mixedwood boreal forest							
Sphyrna lewini	Scalloped Hammerhead	Carcharhiniformes	Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean	Myers et al.	2007	Science	Abundance	No secondary response	Post-hoc	meta-analysis
Sprattus sprattus	European Sprat	Clupeiformes	Human-induced Trophic Cascades and Ecological Regime Shifts in the Baltic Sea	Österblom et al.	2007	Ecosystems	Biodiversity	Chemical and Energy Cycling	Post-hoc	Determined from literature assessment
Squalus acanthias	Spiny Dogfish	Squaliformes	Existing biodiversity, non-indigenous species, food-web and seafloor integrity GEnS indicators. DEVOTES FP7 Project	Teixeira et al.	2014	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Stegastes Fasciolatus	Yelloweye Damselfish	Perciformes	Damselfish as Keystone Species in Reverse: Intermediate Disturbance and Diversity of Reef Algae	Hixon and Brostoff	1983	Science	Behavioral	Biodiversity	Primary	Empirical observation or experiment
Sturnira lilium	Little yellow shouldered Bat	Chiroptera	Keystone species in seed dispersal networks are mainly determined by dietary specialization	Mello et al.	2015	Oikos	Abundance	No secondary response	Primary	network
Sylvilagus palustris	Marsh rabbit	Lagomorpha	Invasive pythons, not anthropogenic stressors, explain the distribution of a keystone species	Sovie et al.	2016	Biological Invasions	Behavioral	No secondary response	Post-hoc	Determined from literature assessment
Theragra chalcogramma	Alaska Pollock	Gadiformes	Anadromous Fish as Keystone Species in	Wilson and Halupka	1995	Conservation Biology	Abundance	No secondary response	Post-hoc	Determined from literature assessment

			Vertebrate Communities							
Thomomys bottae	Botta's Pocket Gopher	Rodentia	Importance of Belowground Herbivory: Pocket Gophers May Limit Aspen to Rock Outcrop Refugia	Cantor and Whitman	1989	Ecology	Abundance	No secondary response	Primary	Empirical observation or experiment
Thunnus albacares	Yellowfin Tuna	Scombriformes	Existing biodiversity, non-indigenous species, food-web and seafloor integrity GEnS indicators. DEVOTES FP7 Project	Teixeira et al.	2014	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Thunnus thynnus	Atlantic Bluefin Tuna	Scombriformes	Existing biodiversity, non-indigenous species, food-web and seafloor integrity GEnS indicators. DEVOTES FP7 Project	Teixeira et al.	2014	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Tursiops truncatus	Common Bottlenose Dolphin	Cetartiodactyla	Overfishing drives a trophic cascade in the Black Sea	Daskalov	2022	Marine Ecology Progress Series	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Tursiops truncatus ponticus	Black Sea Bottlenose Dolphin	Cetartiodactyla	Overfishing drives a trophic cascade in the Black Sea	Daskalov	2022	Marine Ecology Progress Series	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Ultracoelostoma assimile	Sooty Beech Scale	Hemiptera	Beech honeydew: Seasonal variation and use by wasps, honey bees, and other insects	Moller and Tilley	1989	New Zealand Journal of Zoology	Biodiversity	Physical Effects	Primary	Empirical observation or experiment
Ultracoelostoma brittini	Beech Scale	Hemiptera	Beech honeydew: Seasonal variation and use by wasps, honey bees, and other insects	Moller and Tilley	1989	New Zealand Journal of Zoology	Biodiversity	Physical Effects	Primary	Empirical observation or experiment

Uncia uncia	Snow leopard	Carnivora	Restoring a keystone predator may endanger a prey species in a human-altered ecosystem: the return of the snow leopard to Sagarmatha National Park	Lovari et al.	2009	Animal Conservation	Abundance	No secondary response	Primary	Empirical observation or experiment
Upogebia pusilla	Mud shrimp	Eucarida	Bulgarian Initial assessment and GES Report.	BSBD	2013	NA	Abundance	No secondary response	Post-hoc	Determined from literature assessment
Urobatis halleri	Round Stingray	Myliobatiformes	Modeling trophic interactions to assess the effects of a marine protected area: case study in the NW Mediterranean Sea	Valls et al.	2012	Marine Ecology Progress Series	Abundance	No secondary response	Primary	network
Ursus arctos	Brown Bear	Carnivora	A multidecade experiment shows that fertilization by salmon carcasses enhanced tree growth in the riparian zone	Quinn et al.	2018	Ecology	Chemical and Energy Cycling	Life History	Primary	Empirical observation or experiment
Xenopipo atronitens	Black Manakin	Passeriformes	Black Manakin (Xenopipo atronitens) as a keystone species for seed dispersal in a white-sand vegetation enclave in Southwest Amazonia	Santos et al.	2022	Community Ecology	Abundance	Biodiversity	Primary	network
Xerus inauris	Cape Ground Squirrel	Rodentia	Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands	Davidson et al.	2014	Frontiers in Ecology and the Environment	Physical Effects	No secondary response	Post-hoc	Determined from literature assessment