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REVIEW ARTICLE

Ecosystem-level effects of keystone species reintroduction: a literature review

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The keystone species concept was introduced in 1969 in reference to top-down regulation of communities by predators, but has expanded to include myriad species at different trophic levels. Keystone species play disproportionately large, important roles in their ecosystems, but human-wildlife conflicts often drive population declines. Population declines have resulted in the necessity of keystone species reintroduction; however, studies of such reintroductions are rare. We conducted a literature review and found only 30 peer-reviewed journal articles that assessed reintroduced populations of keystone species, and only 11 of these assessed ecosystem-level effects following reintroduction. Nine of 11 publications assessing ecosystem-level effects found evidence of resumption of keystone roles; however, these publications focus on a narrow range of species. We highlight the deficit of peer-reviewed literature on keystone species reintroductions, and draw attention to the need for assessment of ecosystem-level effects so that the presence, extent, and rate of ecosystem restoration driven by keystone species can be better understood.

Key words: ecosystem restoration, ecosystem-level effects, keystone species, population declines, reintroduction

Implications for Practice

- More research into ecosystem-level effects of keystone species reintroduction is required to fully understand if, and to what extent, keystone species act as a restoration tool.
- Studies of keystone species reintroductions should take time lags into account so that delays in ecosystem response time are not misinterpreted as a lack of response.
- Studies of ecosystem-level effects must broaden their range of focal keystone taxa, and their geographical region of interest to better represent areas of greatest research need.

Introduction

The keystone species concept was first introduced in 1969 as an explanation of the disproportionately large top-down influence that purple sea stars (*Pisaster ochraceus*) and sea snails (*Charonia* spp.) imposed on their communities (Paine 1966, 1969). Although originally focused on top predators, the keystone species concept has evolved to include myriad species at different trophic levels (Mills et al. 1993; Power et al. 1996). The current and most broadly accepted definition of keystone species can be summarized as such: species that maintain the organization, stability, and function of their communities, and have disproportionately large, inimitable impacts on their ecosystems (Mills et al. 1993; Power et al. 1996; Kotliar 2000; Delibes-Mateos et al. 2011). Gray wolves (*Canis lupus*), sea otters (*Enhydra lutris*), kangaroo rats (*Dipodomys* spp.), and prairie dogs (*Cynomys* spp.) are some examples of keystone species in their ecosystems. Wolves prevent ungulate overpopulation, and in doing so prevent overbrowsing of vegetation (McLaren & Peterson 1994), and provide scavengers with carrion in winters (Wilmers et al. 2003). Sea otters consume sea urchins (*Strongylocentrotus* spp.), thereby maintain the integrity of the kelp forest's community structure (Mills et al. 1993). Kangaroo rats and prairie dogs modify their habitat, thus influencing other species and ecosystem processes (e.g. nutrient cycling; Whicker & Detling 1988; Krogh et al. 2002), and serve as an important prey source for many avian and terrestrial carnivores (Kotliar et al. 1999).

Keystone species perform essential ecological functions (hereafter referred to as keystone roles), but anthropogenic factors often drive declines in keystone species' populations (Delibes-Mateos et al. 2011). Sea otters were overexploited in the early twentieth century for the fur trade, which led to their near extinction (Ravalli 2009), gray wolves in the United States were intensively hunted following European settlement due to negative depiction in folklore, and frequent livestock depredation resulting from market hunters overharvesting native prey (Fritts et al. 2010), and prairie dogs have been eliminated from most of their former range in North America due to habitat loss and perceived pest status by ranchers (Hoogland 1995).

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In addition to anthropogenic factors, keystone species declines may be driven by natural processes. For example, recent increases in orca (*Orcinus orca*) predation on sea otters (likely driven by a decline in great whales, an important orca prey guild; Estes et al. 2009) have resulted in population declines (Estes et al. 2004), and prairie dog populations are often locally extirpated following disease outbreaks (i.e. sylvatic plague, *Yersinia pestis*; Cully et al. 2006). Although natural processes contribute to keystone species population declines, anthropogenic factors are often the ultimate driver (e.g. orca prey was reduced by whaling, Springer 2003, and sylvatic plague was introduced to the United States around 1900; Cully et al. 2006).

Keystone species affect a multitude of other species and processes in their ecosystems, hence their removal, either naturally or anthropogenically, can have a multitude of effects (see Delibes-Mateos et al. 2011). Anthropogenically driven population declines have resulted in a need to restore keystone species populations. One common method of restoration is translocation, the movement of living organisms from one area with free release in another (IUCN 1987). Translocation has three forms: (1) Introduction: intended or unintended movement of an organism out of its native range; (2) Reintroduction: intended movement of an organism into native range from which it has been extirpated; and (3): Restocking: movement of members of a species to augment the number of individuals in an original habitat (IUCN 1987). Managers have increasingly used keystone species translocations as a tool for conservation benefits, such as restoration of important processes to ecosystems (IUCN/SSC 2013; Cortés-Avizanda et al. 2015; Plein et al. 2016).

Literature reviews that focus on keystone species typically address the function of species in their ecosystems (Kotliar et al. 1999; Janiszewski et al. 2014), the definition of keystone species (Mills et al. 1993; Kotliar 2000; Mouquet et al. 2012), or methods of reintroduction (Truett et al. 2001). Because keystone species reintroduction is proposed as a conservation tool (Cortés-Avizanda et al. 2015; Plein et al. 2016), we desired to review and synthesize the extent, efficacy, and success of keystone species reintroductions. Furthermore, we sought to ascertain the current state of knowledge of the ecosystem-level effects (i.e. effects on other species and ecosystem processes such as, but not limited to, nutrient cycling and hydrological processes) of keystone species reintroductions.

Methods

We conducted our literature review using a topic search in the Web of Science database because of the breadth of scientific fields and dates encompassed (Falagas et al. 2008). We imposed no restrictions on time period except an end date of 2016, and began with a general search for the exact term "keystone species," then narrowed our search to focus on reintroduction of keystone species. We only used terms that referred to the movement of species within their native range, so we conducted literature searches with the following combinations of terms: keystone and restor*, keystone and translocat*, keystone and reintro*, keystone and re-intro*, keystone and reest*, keystone and re-est*, keystone and re est*, keystone and restock*, and keystone and re-stock*. Asterisks were used in Web of Science to represent words with multiple forms (e.g. reintro* includes reintroduce, reintroduced, reintroducing, and reintroduction). When we located publications discussing reintroduction, reestablishment, or translocation of keystone species, we entered title, year of publication, focal taxa, location of study, if the focal taxa were reintroduced, and focus of study (e.g. population dynamics, behavior, etc.) into a database. We excluded publications that focused on species substitutions, movement of species outside of their native range, and invasive species.

We used JMP version 12 to perform statistical analyses. We performed linear regression with year as the explanatory variable and number of publications as the dependent variable to determine if number of publications changed over time.

Table 1. Publications assessing ecosystem-level effects of keystone species reintroductions with description of keystone taxon of interest and aspects assessed in study.

Authors (Year)	*Focal Keystone Taxon*	*Subject*
Mittelbach et al. (1995)	*Micropterus salmoides*	Effects of removal and reintroduction
Le Floc'H et al. (1999)	*Plantago albicans, Stipa lagascae, Cenchrus ciliaris, Rhanterium suaveolens*	Ecosystem restoration
Wilmers et al. (2003)	*Canis lupus*	Provision of carrion to scavengers
Prober and Lunt (2009)	*Themeda australis*	Effects on soil nitrate and exotic invasions
Lovari et al. (2009)	*Uncia uncia*	Effects on prey populations
Ciechanowski et al. (2011)	*Castor* spp.	Effects on vespertilionid bats
Kowalczyk et al. (2011)	*Bison bonasus*	Effects on treestand
Fariñas-Franco et al. (2013)	*Modiolus modiolus*	Effects on community succession
Law et al. (2014)	*Castor* spp.	Effects on macrophytes
Fulgham and Koprowski (2016)	*Cynomys ludovicianus*	Effects on *Dipodomys spectabilis* foraging
Puttock et al. (2017)	*Castor* spp.	Effects on hydrological processes

Results

We found 1,178 publications that include the term "keystone species" in the topic. Among these, only 69 discussed reintroductions. Of the publications that discussed keystone species and reintroduction, 30 focused on populations that had been reintroduced to an area, and 11 assessed ecosystem-level effects of such reintroductions (Table 1; Fig. 1). Publication dates ranged from 1995 to 2016, with between one and eight publications per year, and the number of publications increased with

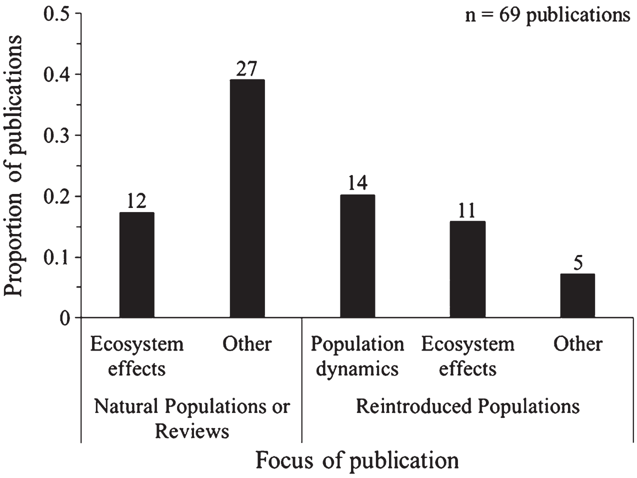

Figure 1. Publication topics and their relative proportion of 69 publications on keystone species reintroductions. Values above each bar indicate number of publications.

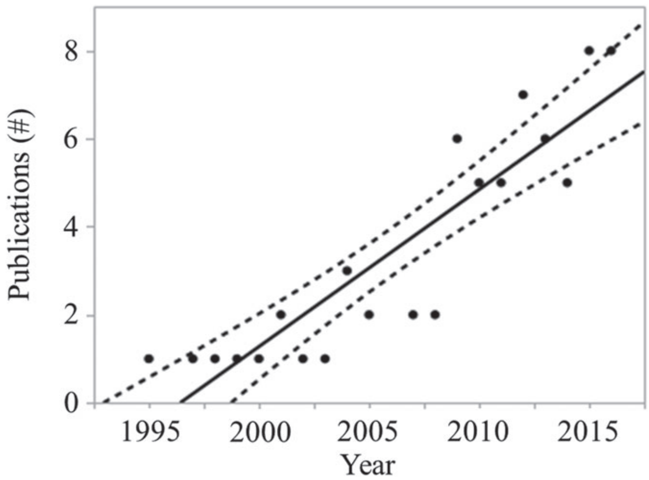

Figure 2. Number of publications on keystone species reintroductions in relation to year (1995–2016). Dotted lines represent 95% confidence intervals.

year ($F_{[1,19]} = 75.71$, $R^2 = 0.81$, $p < 0.001$; Fig. 2). Forty-seven different focal taxa were studied in the 69 publications on keystone species reintroductions; however, only 11 taxa were the subject of more than one publication (Table 2). Four of five categories of keystone species (keystone predator, keystone prey, keystone plant, keystone link, keystone modifier; Mills et al. 1993) were represented in this literature, but most publications (35%) focused on keystone modifiers (keystone links were absent; Fig. 3). Over half of the publications (54%) focused on mammals (Fig. 4) and the majority (42%) focused on keystone species found in the United States (Fig. 5). Keystone species inhabiting 21 ecosystems were addressed in the 69 publications, but 50% focused on species in just four ecosystems (forest, riparian, grassland, and Mediterranean; Fig. 6). Of the 11 publications focusing on ecosystem-level effects of reintroduced keystone species, nine assessed effects of keystone species on other species, and two assessed effects on ecosystem processes such as soil characteristics and hydrological processes. Nine of the 11 publications found evidence of the resumption of keystone roles (influence on other species and their ecosystem), one found negative effects on prey species, and one found no effect. Additionally, studies assessing ecosystem-level effects were conducted 14.40 ± 5.60 years (mean ± SE; range = 1–56 years) following reintroduction of the focal keystone species. Studies documenting resumption of keystone roles were conducted 10.3 ± 3.97 years (mean ± SE; range = 1–36 years) following reintroduction of the focal keystone species, and all but two were conducted at least 5 years post-reintroduction.

Discussion

Anthropogenic movement of organisms has taken place for millennia, but conservation-based reintroductions, especially of keystone species (Cortés-Avizanda et al. 2015), are a relatively new conservation practice (Seddon et al. 2007). Early reintroduction efforts often resulted in failure due to lack of planning, so managers and researchers have applied more rigorous scientific approaches in preparation for and implementation of reintroductions (Shier 2015). The necessity of science-based approaches can be illustrated by two attempts to reintroduce black-tailed prairie dogs (*Cynomys ludovicianus*) to southeastern Arizona. The first reintroduction was attempted in 1972, but was unsuccessful ostensibly due to disagreement about release sites and methods (Brown et al. 1974) that resulted in prairie dogs being released on the landscape without site preparation (i.e. no clearing of vegetation or artificial burrow installation; D. E. Brown 2012, Arizona State University, personal communication). The next effort to reintroduce black-tailed prairie dogs in 2008 was based on extensive research into habitat requirements and suitable sites for reintroduction (Coates 2005), involved collaboration among many stakeholders, and followed thorough guidelines for site preparation, procurement of an adequate number of founder individuals, and release of animals onto the landscape (Underwood & Van Pelt 2000). The scientific rigor applied to the second attempt at black-tailed prairie dog reintroduction proved effective, as the reintroduction effort has resulted in a sustained population of black-tailed prairie dogs within their former range (Hale 2017).

Prior to 1995, peer-reviewed articles focused on keystone species reintroduction were absent from the literature, likely due to the novelty of reintroduction biology (Seddon et al. 2007). Over time, however, the number of publications on keystone species reintroductions has increased with the necessity of reintroduction as a conservation tool (Shier 2015) and the desire for more research-based approaches to reintroductions (Seddon et al. 2007). Although articles discussing keystone species reintroduction have become more common ($n = 69$), most focus on restoration recommendations, environmental needs, and behavior of existing or theoretical populations, whereas few studies have assessed reintroduced populations. Studies that do assess reintroduced populations of keystone species most often focus on population dynamics, which provide valuable information

Table 2. Focal taxa of publications discussing keystone species and reintroduction, reestablishment, or translocation in order from most common to least common.

Focal Taxon	*Publications (No.)*	*Common Name*	*Group*
Castor spp.	9	Beaver	Mammal
Oryctolagus cuniculus	7	European Rabbit	Mammal
Cynomys	4	Prairie Dog	Mammal
Canis lupus	3	Gray Wolf	Mammal
Panthera leo	3	African Lion	Mammal
Enhydra lutris	2	Sea Otter	Mammal
Acropora cervicornis	2	Staghorn Coral	Coral
Castanea dentata	2	American Chestnut	Tree
Ficus spp.	2	Ficus Tree	Tree
Pinus albicaulis	2	Whitebark Pine	Tree
Salvelinus namaycsh	2	Lake Trout	Fish
Pelecanoides urinatrix	1	Common Diving-petrel	Bird
Micropterus salmoides	1	Largemouth Bass	Fish
Sander vitreus	1	Walleye	Fish
Aristida stricta	1	Pineland Threeawn	Grass
Cenchrus ciliaris	1	Buffelgrass	Grass
Stipa lagascae	1	Alatham (Algeria)	Grass
Themeda australis	1	Kangaroo Grass	Grass
Coelostomidia zealandica	1	Great Giant Scale	Insect
Bison bison	1	American Bison	Mammal
Bison bonasus	1	European Bison	Mammal
Canidae	1	Wild Canids	Mammal
Canis lupus dingo	1	Dingo	Mammal
Crocuta crocuta	1	Spotted Hyena	Mammal
Dipodomys spectabilis	1	Banner-tailed Kangaroo Rat	Mammal
Equus ferus	1	Horse	Mammal
Uncia uncia	1	Snow Leopard	Mammal
Crassostrea virginica	1	Oyster	Mollusk
Modiolus modiolus	1	Horsemussel	Mollusk
Bryum pseudotriquetrum	1	Bryum Moss	Moss
Campylium stellatum	1	Star Campylium Moss	Moss
Sphagnum	1	Sphagnum Moss	Moss
Sphagnum warnstorfii	1	Warnstorf's Peat Moss	Moss
Tomenthypnum nitens	1	Tomenthyptnum Moss	Moss
Gopherus polyphemus	1	Gopher Tortoise	Reptile
Carex spp.	1	Sedges	Sedge
Gahnia radula	1	Thatch Saw Sedge	Sedge
Lepidosperma concavum	1	Sandhill Swordsedge	Sedge
Lepidosperma laterale	1	Variable Swordsedge	Sedge
Ceroxylon echinulatum	1	Palm	Tree
Pinus chiapensis	1	Chiapas Pine	Tree
Pinus elliottii	1	Slash Pine	Tree
Acacia spp.	1	Acacia Shrub	Woody Plant/Shrub
Artemisia tridentata wyomingensis	1	Wyoming Big Sagebrush	Woody Plant/Shrub
Banksia attenuata	1	Candlestick Banksia	Woody Plant/Shrub
Plantago albicans	1	Plantain	Woody Plant/Shrub
Rhanterium suaveolens	1	Arfadja	Woody Plant/Shrub

to managers about the success or failure of reintroduction and allow early detection of problems (Long et al. 2006; Hale 2017), but assessment of ecosystem-level effects after keystone species reintroductions is lacking. Our literature search only returned 11 publications that assessed the ecosystem-level effects of the reintroduction of keystone species, and of those, three focused on beavers (*Castor* spp.). After reintroduction, beavers resume several keystone functions, such as influencing hydrological processes and space use of bats (Ciechanowski et al. 2011; Law et al. 2014), but there is a dearth of information on how other keystone species affect their ecosystems following reintroduction, as only 11 taxa have been investigated, and most are only the subject of a single study.

Keystone species in situ substantially influence their ecosystems (Whicker & Detling 1988; Mills et al. 1993; McLaren & Peterson 1994; Hoogland 1995; Kotliar et al. 1999; Wilmers et al. 2003; Cosentino et al. 2014), hence, their removal may have cascading effects (Sarnelle 1992; Mittelbach et al. 1995;

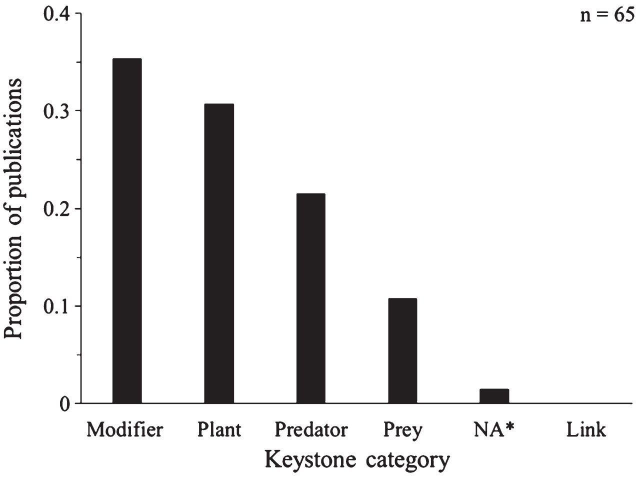

Figure 3. Categories of keystone species (after Mills et al. 1993) studied in publications, and the relative proportion of each category focused on. Some studies did not have a focal keystone species ($n < 69$).

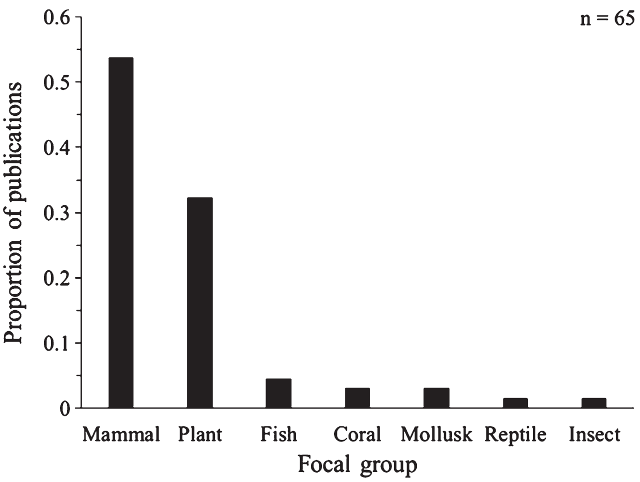

Figure 4. Groups of taxa to which focal keystone species belong, and the proportion of studies that examine a keystone species within each group. Some studies did not have a focal keystone species ($n < 69$).

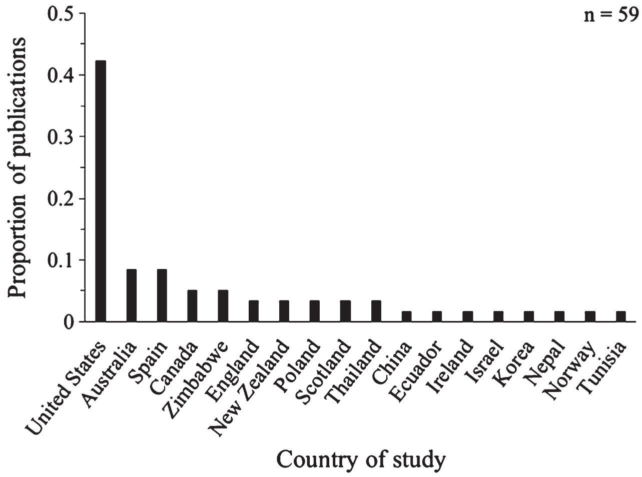

Figure 5. Countries in which studies were conducted, and their relative proportions of studies which occurred in specific geographic locales. Some studies did not have specific locales (e.g. literature reviews; $n < 69$).

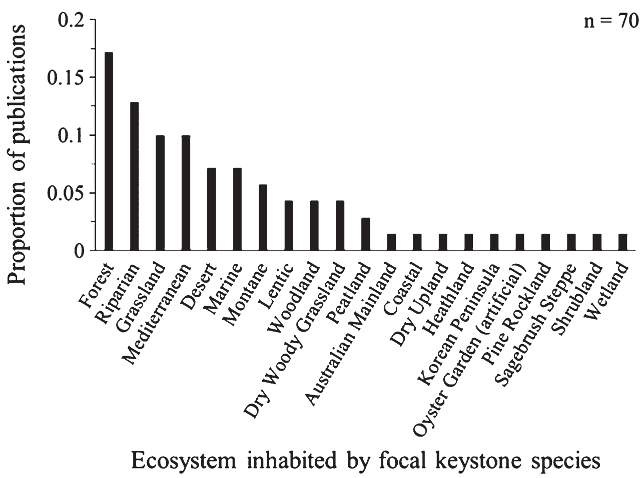

Figure 6. Ecosystems inhabited by focal keystone species of study, and the relative proportion of publications focusing on specific ecosystems. Some studies examined more than one ecosystem ($n > 69$).

Estes et al. 2004; Ceballos et al. 2010; Martínez-Estévez et al. 2013). For example, in Alaska, after sea otter populations declined, previously dense kelp forests upon which many fish and invertebrate species relied (Schiel & Foster 2015) were denuded by sea urchins, the preferred prey of sea otters (Estes et al. 2004). Additionally, the removal of a top predator, the largemouth bass (*Micropterus salmoides*), from a Michigan lake allowed an increase in zooplanktivorous fish that had previously been consumed by bass, which resulted in a decrease in zooplankton (*Daphnia* spp.) that maintained water clarity (Mittelbach et al. 1995) and suppressed eutrophication (Sarnelle 1992). Finally, declines in prairie dog populations in Mexico have resulted in shrub invasion (Ceballos et al. 2010) and desertification of previously occupied prairie dog colonies via soil compaction, increased erosion, reduced water infiltration, reduced soil carbon storage capacity, and reduced herbaceous biomass (Martínez-Estévez et al. 2013).

While much is known about keystone species and effects of their removal, it is unknown if, when, and to what extent keystone species can resume their roles following reintroduction, especially after prolonged absence. Managers often justify keystone reintroductions based on the anticipated or assumed benefits to the ecosystem (Underwood & Van Pelt 2000; Stringer & Gaywood 2016), but actual ecosystem responses to keystone species reintroductions are poorly understood and rarely assessed, indicated by only 0.9% of keystone species publications that focus on ecosystem-level effects of reintroductions. Furthermore, nine publications discussed evidence of the resumption of keystone roles, and all but two were conducted five or more years post-reintroduction. This suggests that ecosystem-level responses may not immediately be detected after reintroduction of keystone species. Lags in ecosystem-level responses to keystone species reintroductions indicate that certain aspects of keystone functions may resume at different rates, suggesting that delayed responses may not be detected in the duration of study, and may be interpreted as lack of response. For example, prairie dogs physically modify their environments by burrowing, which turns soil and cycles nutrients (Whicker & Detling 1988). After reintroduction, prairie dogs would likely resume their role of nutrient cycling immediately through burrowing activities, but the influence on the biotic community (e.g. small mammals and vegetation) may not be manifested in the short term (Davidson et al. 1999), which could be interpreted as prairie dogs' inability to resume their keystone role. It is important to understand not only potential ecosystem-level outcomes prior to implementation of keystone species reintroduction as a management tool but also the timeline of occurrence so that effects may be accurately assessed and interpreted.

In addition to the aim of keystone species studies, focal taxa and geographical region need to be broadened. Over half of the studies that focused on keystone species reintroductions were conducted on mammals, and the largest percentage of studies took place in the United States. Our results are likely an artifact of preexisting biases in the conservation literature as a whole toward mammals (Clark & May 2002) and the United States (Wilson et al. 2016). Mammals are typically overrepresented in the literature because they are charismatic and may increase awareness of broader conservation efforts, which in turn benefits less charismatic species (Clark & May 2002; Cronin et al. 2014); however, the bias toward studies conducted in the United States is more complicated. Several factors contributing to a geographical bias are costs of open access publication, representation in international forums, and access to social media, which have led to countries with the greatest biodiversity, and research need, being underrepresented in the literature (Wilson et al. 2016).

Our review highlights the deficit of peer-reviewed articles that assess ecosystem-level consequences of keystone species reintroductions, a bias toward mammals as a focal taxon, and a bias toward studies conducted in the United Sates. While studies of population dynamics of reintroduced keystone species are important to inform managers about the success of reintroductions (Long et al. 2006; Hale 2017), more studies must focus on ecosystem-level effects of reintroductions (Robert et al. 2015) so that the presence, extent, and rate of ecosystem restoration driven by keystone species can be understood. Additionally, studies conducted on a wider variety of taxonomic groups, and in other geographic regions, would add to the understanding of keystone species worldwide, and increase knowledge in areas of high conservation concern where studies are lacking. Studies of ecosystem-level effects will better inform managers as to whether keystone species can resume their roles following reintroduction, whether their roles are singular or part of an interacting complex of keystone species in the system, and will provide new insights into ecosystem management or restoration through the reintroduction of a single species.

LITERATURE CITED

Brown DE, Todd RL, Levy SH (1974) Proposal for the reintroduction of the black-tailed prairie dog into Arizona, (Project W-53-R-24). Arizona Small Game Investigations, Arizona Game and Fish Department, Phoenix, Arizona

Ceballos G, Davidson A, List R, Pacheco J, Manzano-Fischer P, Santos-Barrera G, Cruzado J (2010) Rapid decline of a grassland system and its ecological and conservation implications. PLoS One 5:e8562

Ciechanowski M, Kubic W, Rynkiewicz A, Zwolicki A (2011) Reintroduction of beavers *Castor fiber* may improve habitat quality for vespertilionid bats foraging in small river valleys. European Journal of Wildlife Research 57:737–747

Clark JA, May RM (2002) Taxonomic bias in conservation research. Science 297:191–192

Coates CA (2005) Suitability of potential habitat for the extirpated Arizona black-tailed prairie dog. MS thesis. University of Arizona, Tucson

Cortés-Avizanda A, Colomer MÀ, Margalida A, Ceballos O, Donázar JA (2015) Modeling the consequences of the demise and potential recovery of a keystone-species: wild rabbits and avian scavengers in Mediterranean landscapes. Scientific Reports 5:17033

Cosentino BJ, Schooley RL, Bestelmeyer BT, Kelly JF, Coffman JM (2014) Constraints and timelags for recovery of a keystone species (*Dipodomys spectabilis*) after landscape restoration. Landscape Ecology 29:665–675

Cronin DT, Owens JR, Choi H, Hromada S, Malhotra R, Roser F, Bergl RA (2014) Where has all our research gone? A 20-year assessment of the peer-reviewed wildlife conservation literature. International Journal of Comparative Psychology 27:101–116

Cully JF, Biggins DE, Seerey DB (2006) Conservation of prairie dogs in areas with plague. Pages 157–168. In: Hoogland JL (ed) Conservation of the black-tailed prairie dog: saving North America's western grasslands. Island Press, Washington D.C.

Davidson AD, Parmenter RR, Gose JR (1999) Responses of small mammals and vegetation to a reintroduction of Gunnison's prairie dogs. Journal of Mammalogy 80:1311–1324

Delibes-Mateos M, Smith AT, Slobodchikoff CN, Swenson JE (2011) The paradox of keystone species persecuted as pests: a call for the conservation of abundant small mammals in their native range. Biological Conservation 144:1335–1346

Estes JA, Danner EM, Doak DF, Konar B, Springer AM, Steinberg PD, Tinker MT, Williams TM (2004) Complex trophic interactions in kelp forest ecosystems. Bulletin of Marine Science 74:621–638

Estes JA, Doak DF, Springer AM, Williams TM (2009) Causes and consequences of marine mammal population declines in southwest Alaska: a food-web perspective. Philosophical Transactions of the Royal Society B 364:1647–1658

Falagas ME, Pitsouni EI, Malietzis GA, Pappas G (2008) Comparison of PubMed, Scopus, Web of Science, and Google Scholar: strengths and weaknesses. The FASEB Journal 22:338–342

Fariñas-Franco JM, Allcock L, Smyth D, Roberts D (2013) Community convergence and recruitment of keystone species as performance indicators of artificial reefs. Journal of Sea Research 78:59–74

Fritts SH, Stephenson RO, Hayes RD, Boitani L (2010) Wolves and humans. Pages 289–316. In: Mech LD, Boitani L (eds) Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois

Fulgham KM, Koprowski JL (2016) Kangaroo rat foraging in proximity to a colony of reintroduced black-tailed prairie dogs. Southwestern Naturalist 61:194–202

Hale SL (2017) Active management contributes to successful reintroduction of a keystone species: black-tailed prairie dog (*Cynomys ludovicianus*) return to grasslands. PhD dissertation. University of Arizona, Tucson

Hoogland JL (1995) The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois

IUCN (1987) Position statement on translocations of living organisms: introductions, reintroductions, and re-stocking. International Union for Conservation of Nature and Natural Resources Council, Gland, Switzerland

IUCN/SSC (2013) Guidelines for reintroductions and other conservation translocations. IUCN Species Survival Commission, Gland, Switzerland

Janiszewski P, Hanzal V, Misiukiewicz W (2014) The Eurasian beaver (*Castor fiber*) as a keystone species – a literature review. Baltic Forestry 20:277–286

Kotliar NB (2000) Application of the new keystone-species concept to prairie dogs: how well does it work? Conservation Biology 14:1715–1721

Kotliar NB, Baker BW, Whicker AD (1999) A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24:177–192

Kowalczyk R, Taberlet P, Coissac E, Valentini A, Miquel C, Kamiński T, Wójcik JM (2011) Influence of management practices on large herbivore diet-case of European bison in Białowieża Primeval Forest (Poland). Forest Ecology and Management 261:821–828

Krogh SN, Zeisset MS, Jackson E, Whitford WG (2002) Presence/absence of a keystone species as an indicator of rangeland health. Journal of Arid Environments 50:513–519

Law A, Jones KC, Willby NJ (2014) Medium vs. short-term effects of herbivory by Eurasian beaver on aquatic vegetation. Aquatic Botany 116: 27–34

Le Floc'H E, Neffati M, Chaieb M, Floret C, Pontanier R (1999) Rehabilitation experiment at Menzel Habib, southern Tunisia. Arid Soil Research and Rehabilitation 13:357–368

Long D, Bly-Honness K, Truett JC, Seery DB (2006) Establishment of new prairie dog colonies by translocation. Pages 188–209. In: Hoogland JL (ed) Conservation of the black-tailed prairie dog: saving North America's western grasslands. Island Press, Washington D.C.

Lovari S, Boesi R, Minder I, Mucci N, Randi E, Dematteis A, Ale SB (2009) Restoring a keystone predator may endanger a prey species in a human-altered ecosystem: the return of the snow leopard to Sagarmatha National Park. Animal Conservation 12:559–570

Martínez-Estévez L, Balvanera P, Pacheco J, Ceballos G (2013) Prairie dog decline reduces the supply of ecosystem services and leads to desertification of semiarid grasslands. PLoS One 8:e75229

McLaren BE, Peterson RO (1994) Wolves, moose, and tree rings on Isle Royale. Science 266:1555–1558

Mills LS, Soulé ME, Doak DF (1993) The keystone-species concept in ecology and conservation. Bioscience 43:219–224

Mittelbach GG, Turner AM, Hall DJ, Rettig JE, Osenberg CW (1995) Perturbation and resilience: a long-term, whole-lake study of predator extinction and reintroduction. Ecology 76:2347–2360

Mouquet N, Gravel D, Massol F, Calcagno V (2012) Extending the concept of keystone species to communities and ecosystems. Ecology Letters 16:1–8

Paine RT (1966) Food web complexity and species diversity. The American Naturalist 100:65–75

Paine RT (1969) A note on trophic complexity and community stability. The American Naturalist 103:91–93

Plein M, Bode M, Moir ML, Vesk PA (2016) Translocation strategies for multiple species depend on interspecific interaction type. Ecological Applications 26:1186–1197

Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. Bioscience 46:609–620

Prober SM, Lunt ID (2009) Restoration of *Themeda australis* swards suppresses soil nitrate and enhances ecological resistance to invasion by exotic annuals. Biological Invasions 11:171–181

Puttock A, Graham HA, Cunliffe AM (2017) Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. Science of the Total Environment 576:430–443

Ravalli R (2009) The near extinction and reemergence of the pacific sea otter, 1850-1938. The Pacific Northwest Quarterly 100:181–191

Robert A, Colas B, Guigon I, Kerbiriou C, Mihoub JB, Saint-Jalme M, Sarrazin F (2015) Reintroducing reintroductions into the conservation arena. Animal Conservation 18:413–414

Sarnelle O (1992) Nutrient enrichment and grazer effects on phytoplankton in lakes. Ecology 73:551–560

Schiel DR, Foster MS (2015) The biology and ecology of giant kelp forests. University of California Press, Oakland

Seddon PJ, Armstrong DP, Maloney RF (2007) Developing the science of reintroduction biology. Conservation Biology 21:303–312

Shier DM (2015) Developing a standard for evaluating reintroduction success using IUCN Red List indices. Animal Conservation 18:411–412

Springer AM (2003) Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? Proceedings of the National Academy of Sciences of the United States of America 100:12223–12228

Stringer AP, Gaywood MJ (2016) The impacts of beavers *Castor* spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK. Mammal Review 46:270–283

Truett JC, Dullum JALD, Matchett MR, Owens E, Seery D (2001) Translocating prairie dogs: a review. Wildlife Society Bulletin 29:863–872

Underwood JG, Van Pelt WE (2000) A proposal to reestablish the black-tailed prairie dog (*Cynomys ludovicianus*) to southern Arizona. Arizona Game and Fish Department, Nongame and Endangered Wildlife Program Draft Technical Report, Phoenix, Arizona

Whicker AD, Detling JK (1988) Ecological consequences of prairie dog disturbances. Bioscience 38:778–785

Wilmers CC, Crabtree RL, Smith DW, Murphy KM, Getz WM (2003) Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology 72:909–991

Wilson KA, Auerbach NA, Sam K, Magini AG, Moss ASL, Langhans SD, Budiharta S, Terzano D, Meijaard E (2016) Conservation research is not happening where it is most needed. PLoS Biology 14:e1002413

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