Review

Examining the factors that influence the strength of keystone interactions

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ABSTRACT

The influence of abiotic and biotic factors on the community-wide impact of keystone species is reviewed. Experiments have shown that environmental factors, such as microclimate, may alter the composition of the community by altering the morphology of the keystone species. Other environmental factors, such as wave action, can increase or decrease the impact of a keystone species on its community. Biotic factors, such as the composition of a community, may also determine whether or not a particular species will take on a keystone role. Other predators may negate the role of one predator as a keystone species, or influence the growth, survival, or impact of a keystone species. The roles of keystone species are often dependent on many abiotic and biotic features of the community and its environment. Therefore, in order to truly understand the role these species play in communities, it is imperative that these features are considered when studying keystone species and their communities.

KEYWORDS: trophic cascade, keystone predator, invasive species, abiotic effects, biotic effects

INTRODUCTION

The concept of keystone species was first popularized in 1969 by Robert T. Paine [1, 2]. Specifically the notion of a keystone predator was initially described as a native species that has the ability to alter physical appearances and species composition of the community [3]. Since the first appearance of this concept, many variations and modifications have been developed, with more recent ones including the idea that the impact of keystone species on the community is disproportionately larger than their abundance [4]. Much controversy surrounds the definition of a keystone species. Many ecologists focus on the trophic cascades that result from the effects of keystone predators on abundances of autotrophs, while others attempt to broaden their research to include other effects such as changes in size or composition of species [5]. While the original focus of the keystone species concept did revolve around predators with the ability to increase biodiversity by preying on dominant species, the concept has broadened to include potential for lowering diversity [4]. Despite the variability among definitions used to characterize keystone species, many ecologists can agree on two general characteristics: keystone species are critical components for sustaining diversity and organization, and their value to the community is relatively greater in comparison to other species [3]. Regardless of the intense focus placed on keystone predators, keystone species are not limited to those deemed of highest trophic rank [6]. For instance, honeydew-producing insects of the genus *Ultracoelostoma* may be regarded as keystone species within beech forest communities in New Zealand [6]. In fact, the keystone species concept has also expanded to encompass other functional groups including the following: modifiers,

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plants, prey species, and link species [3]. Another example of non-predatory keystone species is a mangrove leaf removing crab, *Ucides cordatus*, in Brazil [7]. These crabs play a vital role in these mangrove forests; burial of leaf litter and consumption proved to be the most important process (67%) in the turnover of leaf litter, followed by tidal export (31%) and decomposition (2%) [7]. According to similar studies, large quantities of leaf litter and mangrove propagules can be hidden and consumed by crabs, greatly impacting the pathways of carbon flow through the ecosystem [7]. In regards to identifying keystone species, perturbation experiments are often utilized; a removal of the species in question and close observation of other species is required, as is sufficient replication [3]. Despite the useful nature of these perturbation experiments, it is difficult to complete them in complex, natural systems [3].

While keystone species clearly contribute to the proper functioning of communities and ecosystem processes, questions pertaining to factors responsible for their existence and function exist. What biotic and abiotic factors influence a keystone species' ability to perform an essential role in the community? Other questions can then be developed within the context of the above inquiry: Does a keystone species always perform the same function no matter where it lives, even within invaded communities? How do other members of the community impact the ability of a keystone species to perform its role? What factors can strengthen or weaken interactions between keystone species and the rest of the community?

Rather than solely studying the impact keystone species have on their environment, it is essential to examine how and why interactions among species in a community vary [5]. According to Piraino *et al.* the impact and strength of interactions between keystone species and biotic components of their community can vary with resource availability, prey life history, and environmental conditions [4]. Other factors capable of influencing species interactions include environmental stressors, productivity, and habitat complexity [5]. The strength of keystone effects on an inferior species is also predicted to be stronger when the inferior species is not inhibited

by resource availability, predation, or competition [8]. The following discussion is designed to explore these abiotic and biotic factors that influence the existence and strength of interactions between keystone species and other members of the community.

DISCUSSION

Ecosystem processes and mechanisms are never static. As ecosystems experience perturbations such as fire or flood, spurring on succession, there is potential for new suites of species to inhabit the area [3]. With these changes and progression of succession stages, come new keystone species [3]. Since discrepancies exist between species in regards to tolerances for certain environmental conditions, there is always potential for abiotic factors to influence the ability of a species to serve a keystone role in their community. Climate is, of course, a crucial environmental factor that can dictate the composition of species assemblages. Microclimate, or the climate which an organism is surrounded by and directly exposed to, plays a huge role in shaping distribution of species on the sub-Antarctic Marion Island [9]. The plant species, *Azorella selago*, serves as a keystone species on this island by generating cushions along rocky soils and providing structure and habitat for epiphytes, bryophytes, and invertebrates [9]. Any large-scale climate changes will influence the microclimates on Marion Island and impact the crucial plant assemblages [9]. This study showed that climate varied on eastern and western sides of the island as well as with altitude, exposing *A. selago* to different conditions on both sides [9]. Morphological features of these plants as well as the distribution of arthropods inhabiting the plants differed depending on altitude and side of the island, demonstrating that climate influences these keystone species and the rest of the community [9].

In a study by Menge *et al.* the impacts of environmental conditions on the ability of *Pisaster ochraceus* to serve as a keystone predator in the Pacific intertidal habitats was examined [5]. This sea star is capable of greatly influencing abundances and distribution of *Mytilus californianus*, but this is not always the case [5]. Mussels can have drastic impacts within intertidal areas, quickly outcompeting

other organisms and taking over available substrate; sea stars can mitigate the negative effects of these mussels by actively consuming large quantities [5]. In a manipulative experiment, Menge *et al.* showed that these sea stars can exert enough predation pressure to effectively remove mussels from the low intertidal zone [5]. The strength of their predation effects did vary, however, with stronger predation experienced within areas exposed to waves, and weaker predation in those zones protected from wave impact [5]. Predation in protected habitats varied spatially and temporally, as well, with low recruitment and sand burial appearing to play a role in influencing predatory interactions between *P. ochraceus* and *M. californianus* [5]. Viewing Figure 1, it is clear that survival of *M. californianus* was greater at both sites in the protected areas in the presence of the predatory sea stars than in the presence of the predators at the exposed sites [5]. Additionally, survival of these mussels in the exposed sites was lower in the presence of the keystone predator than in their absence [5]. Both variables, exposure and the predator, *Pisaster*, had statistically significant effects on mussel survival ($p<0.025$ each), with the interactions between the predator and exposure significantly impacting survival of mussels as well ($p<0.05$) [5]. Other studies have revealed positive associations between prey recruitment of *M. californianus* and wave exposure: growth of recruits occurs faster in wave-impacted regions than protected areas, which should increase the odds of predator saturation [10]. Though mussels may grow faster and prefer settling in wave-exposed areas, their survival was negatively impacted in the presence of sea stars in the Menge *et al.* study; the results demonstrate the critical influence of abiotic factors, in this case wave action, on prey recruitment and, ultimately the strength of keystone effects [5]. On the rocky Pacific shore of California, lobsters act as keystone predators by removing competitively dominant mussels which allows red alga communities to thrive. A study conducted by Robles determined that the ability of the spiny lobster, *Panulirus interruptus*, to serve as a keystone predator depends on the level of mussel recruitment [10]. Areas with high wave action showed little recruitment of the mussels, which led to algal assemblages being maintained regardless of the

presence of *P. interruptus* [10]. Thus, the importance of spiny lobster and its effect as a keystone predator depend on the wave action at a site and subsequent differences in mussel recruitments.

Fauth conducted a study concerning the identification of keystone species in ponds and discovered that the identity of a keystone predator varied regionally, by landcape aspects of the ponds and with abiotic factors [11]. The ability of one of the species in the study, *Ambystoma talpoideum*, the mole salamander, to function as a keystone species was independent of both environmental variables and anuran densities as depicted in Figure 2 [11]. Figure 3 depicts the ability of a larval dragonfly species, *Tramea carolina*, to function as keystone species only in those highly acidic ponds with greater anuran densities [11]. While the mole salamander was able to function as a keystone species under varied abiotic and biotic conditions in this particular study, it was hypothesized that the dragonfly larvae were only capable of this role when surrounded by the most favorable conditions for activity and survival [11]. The highly acidic ponds inhabited by *T. carolina* do not typically have any fish and are, therefore, dominated by invertebrates [11]. It follows that these dragonflies would only serve as dominant predators in ponds without fish. This study provides evidence for the notion that the strength of keystone interactions can vary with environmental conditions, and that the degree to which keystone predators are impacted by external factors can vary by species.

As these studies have demonstrated, the status of keystone predators within a community is not only influenced by environmental factors, but can be affected by prey recruitment to the area as well [4]. While some keystone species only exhibit effective predation in areas of high prey recruitment, others exclusively serve the role of keystone predators when prey recruitment rates are low [4]. A study by Estes and Duggins emphasized the importance of size-selective predation by sea otters as well as recruitment of urchins as contributing factors shaping kelp forest communities [12]. Sea otters serve as keystone predators in Alaskan kelp forest communities, preying on sea urchins that graze on kelp [12]. Recruitment rates and sizes of urchins differed
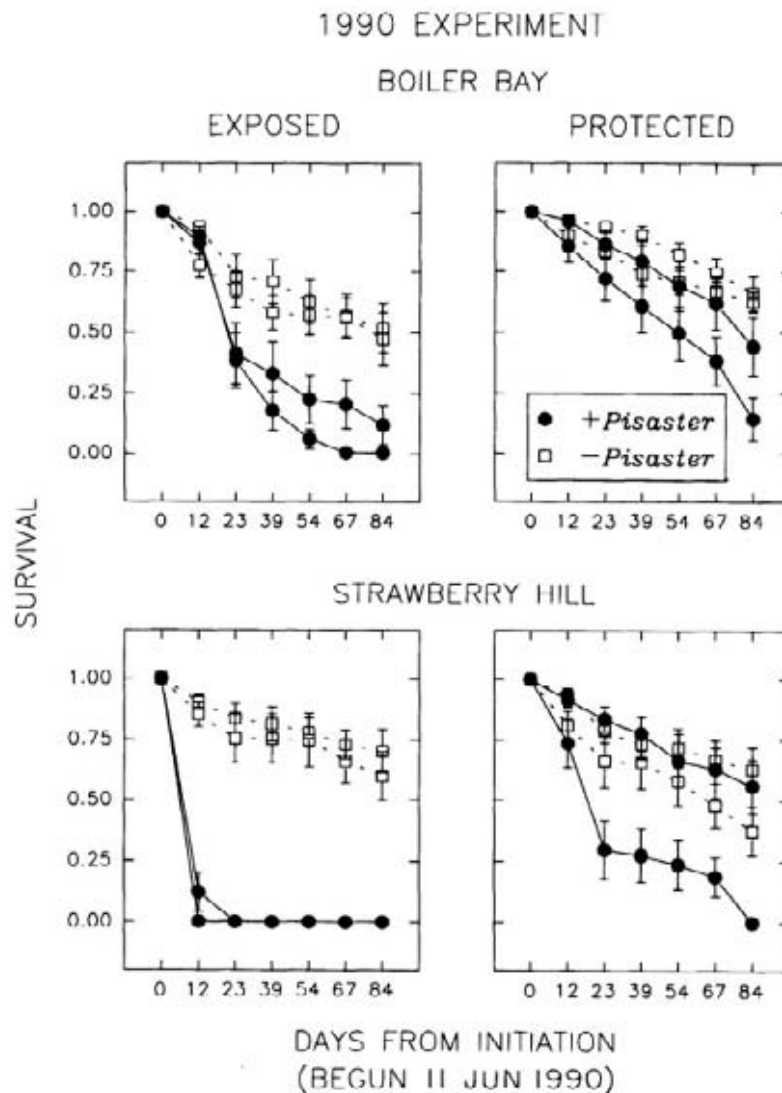
1990 EXPERIMENT

BOILER BAY

EXPOSED   PROTECTED

STRAWBERRY HILL

DAYS FROM INITIATION
(BEGUN 11 JUN 1990)

Figure 1. Mussel (*Mytilus californianus*) transplant experiment in which the number of surviving mussels was determined with (+*Pisaster*) or without (-*Pisaster*) keystone predators under varying wave conditions (exposed or protected). Reprinted from [5] with permission from Ecological Society of America.

geographically between the Aleutian Islands and southeast Alaska, ultimately contributing to discrepancy in the impact of sea otter predation on kelp reforestation [12]. The introduction of sea otters into previously uninhabited areas of southeast Alaska caused quick declines in sea urchin biomass by almost 100%, while dense populations of urchins remaining present on the Aleutian Islands even in the presence of sea otters [12]. Smaller urchins were consistently located in the Aleutian Islands, while southeast Alaska was practically devoid of urchins similar in size.

Sea otters demonstrated consistency in this study by consuming the largest prey available as is shown in Figure 4 [12]. Urchins that are not the preferred size for sea otter predation in the Aleutian Islands continue to proliferate and recruit rapidly, ultimately inhibiting recovery of kelp forests [12]. Recruitment appeared to occur more sporadically in southeast Alaska, however, with gaps of years possible between large recruitment events; differences in oceanic processes may explain this discrepancy [12]. Another potential explanation is that recruitment is comparable among regions,
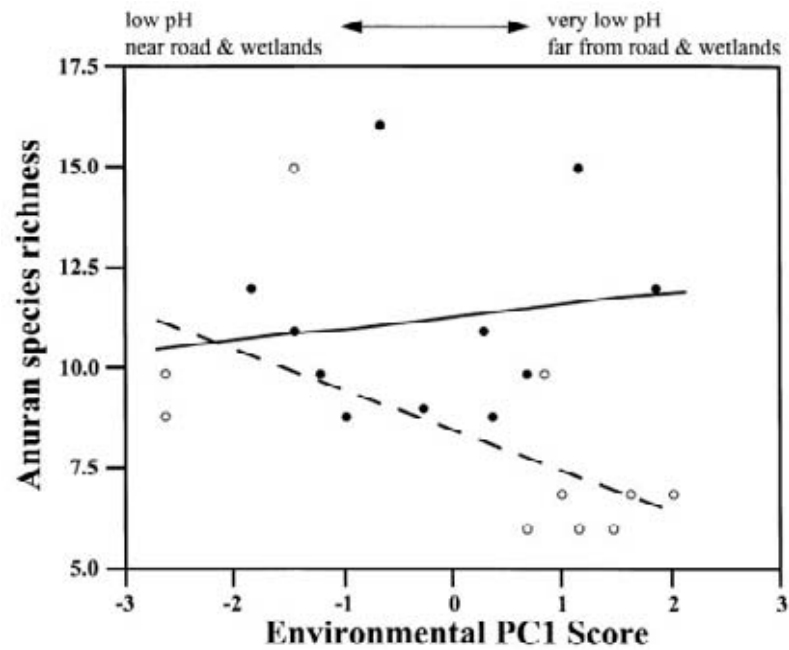
Figure 2. Mole salamanders (*Ambystoma talpoideum*) act as keystone species regulating anuran species diversity regardless of the environmental conditions or anuran densities. The solid line and closed symbols represent ponds with mole salamanders, while the dotted line and open symbols represent ponds without mole salamanders. Reprinted from Fauth, J. 1999, Ecol. Lett., 2, 36 with permission from John Wiley and Sons.
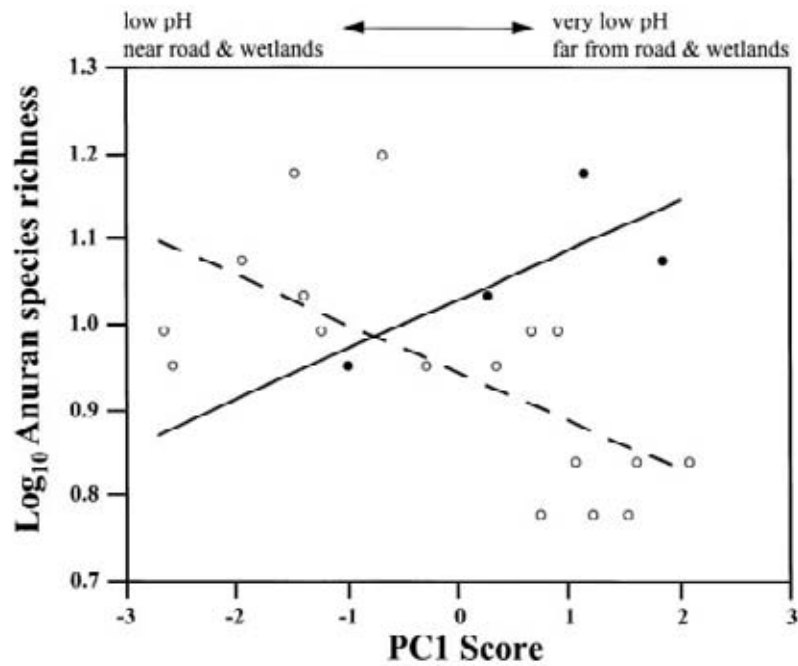

Figure 3. Larval dragonflies (*Tramea carolina*) exhibited context-dependent keystone effects on anuran species diversity. The solid line and closed symbols represent ponds with larval dragonflies, while the dotted line and open symbols represent ponds without larval dragonflies. Reprinted from Fauth, J. 1999, Ecol. Lett., 2, 36 with permission from John Wiley and Sons.
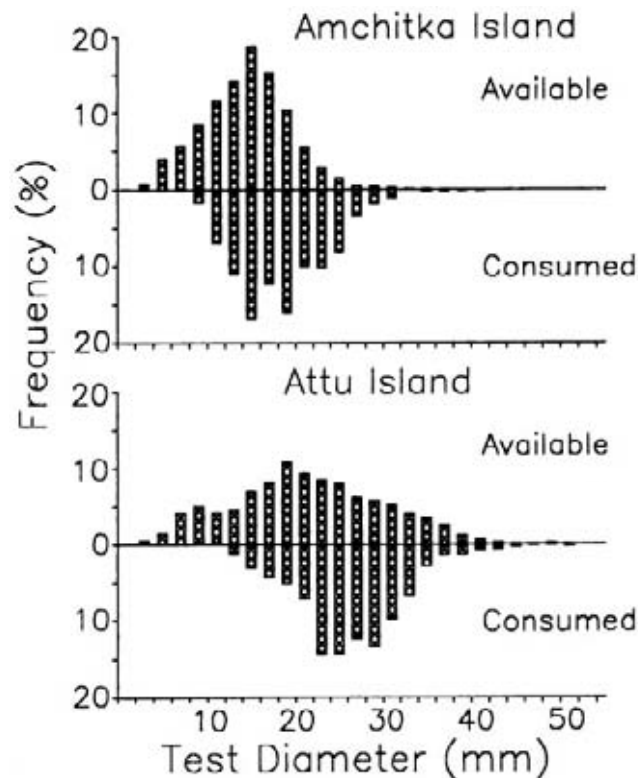
Figure 4. Size distributions of natural populations of *Strongylocentrotus polyacanthus*, sea urchins, available for sea otter predation versus the sizes of sea urchins actually consumed by sea otters at Amchitka and Attu islands. Reprinted from [12] with permission from Ecological Society of America.

but that an additional predator unique to south east Alaska, such as the sunflower sea star, is removing smaller recruits quickly [12]. If this is the case then the alternate predator would be indirectly affecting the actions of the keystone predator and ultimately the health of the kelp forests.

The composition of species within an ecosystem largely determines whether a particular species will take on a keystone role [13]. While life history traits of prey species appear to significantly influence the strength of keystone interactions, studies have also examined the potential influence of other predators on the keystone species [14]. Though not specifically limited to keystone predation, it has been found that the effectiveness of prey capture will greatly depend on the presence of other predators and the behaviors demonstrated by predators sharing the same habitat [15]. Again focusing on the rocky intertidal habitat of the Pacific Northwest, Navarrete and

Menge conducted a study to illustrate the interactive effects between the keystone predator, *Pisaster ochraceus*, and predatory whelks (*Nucella* species). Results attained in this study revealed that the effects of the sea stars on mussels were strong even in the presence of the whelks; the whelks, however, were only capable of significantly impacting mussels in those treatments without sea stars [14]. The interactions between the whelks and sea stars are indirect since sea stars don't appear to be consuming the whelks; it is even possible that in the presence of high densities of sea stars, the whelks will begin feeding on other prey [14]. The results from this study support the idea that the impact of keystone predators on the community will be strong, regardless of the presence of other predators [14]. McClintok *et al.* studied behavioral interactions between three sympatric sea stars and a keystone sea star, *Odontaster validu* [16]. The results revealed that *O. validus* did exhibit changes in behavioral responses in the presence of one of the other

predatory species, *Perknaster auraorae*; the keystone species exhibited greater mean levels of activity [16]. The keystone species also displayed negative responses to *P. aurorae* by immediately turning away upon contact and increasing speeds after the encounter [16]. These behavioral responses indicate the presence of chemotactile responses as well as the potential for chemodetection over greater distances occurring in *O. validus* in response to *P. aurorae* [16]. Results from this study, in contrast with those reported by Navarrete and Menge, do support the idea that other predatory species greatly influence keystone species [16, 14]. Fauth and Resetarits examined interactions between the predator *Notophthalmus viridescens* and another predator, *Siren intermedia* [17]. This study revealed a statistically significant density interaction between *N. viridescens* and *S. intermedia* ($p < 0.0054$) on the survival and growth rates of the keystone species; the impact of *S. intermedia* was dependent on the initial densities of *N. viridescens* [17]. In the presence of *S. intermedia*, the keystone species experienced 25% lower survival when in high densities versus lower densities, and a drop of 62% in growth rates; Figure 5 below demonstrates these patterns, indicating the presence of intense interspecific competition [17]. The presence of the siren also negatively impacted reproduction of the keystone species; reproductive output was reduced by 64% in low-density ponds [17]. Despite the negative

effects on growth, survival, and reproduction, the presence of *S. intermedia* did not inhibit *N. viridesens*' ability to serve as a keystone predator in this ecosystem [17]. The keystone predator still preferentially fed on dominant anurans and was still able to change the species composition, while the other predator did not modify the prey assemblages [17].

In a study by Smith, the interactions between the same keystone predator, *N. viridescens*, and invasive anuran species were examined within mesocosms simulating invaded communities [18]. Though little had been revealed regarding the role of keystone species within invaded communities prior to this study, it was thought that keystone predators could contribute to the maintenance of diversity in invaded communities just as they do in native ones [18]. *N. viridescens*, the eastern newt, selectively preys upon the competitively superior tadpoles in anuran assemblages. Smith's experiment manipulated treatments containing two competitively dominant anurans to see if the newts would prey on the invasive species and maintain the natural balance of the community [18]. The newts switched from feeding on the native dominant species *Bufo terrestris*, to consuming the non-native *Osteopilus septentrionalis* in large quantities [17]. The newts served as keystone predators in the invaded communities, allowing survival of *B. terrestris* to increase as *O. septentrionalis* suffered higher mortality [18].
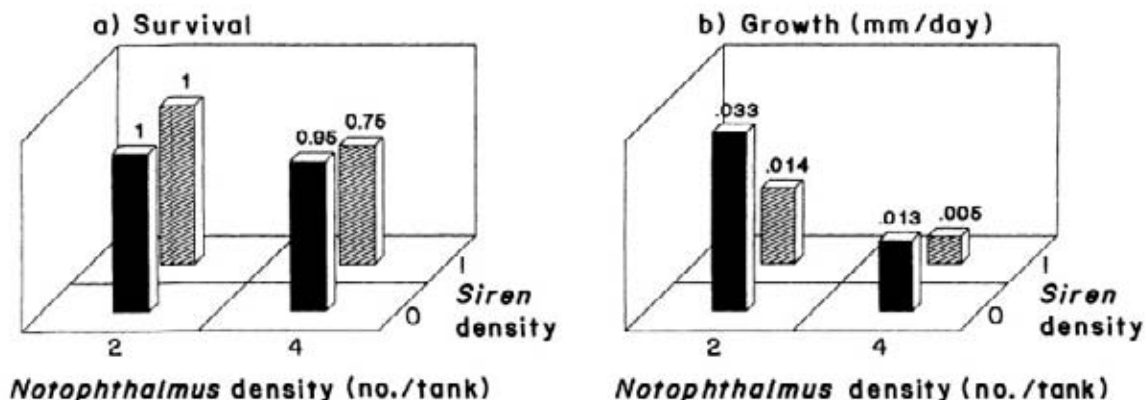

Figure 5. Intense interspecific competition between a keystone predator, *Notophthalus viridescens*, and a competing predator, *Siren intermedia*, led to reduced survival and growth in the keystone species. Bars show the mean poetpulation response for *N. viridescens.* Reprinted from [17] with permission from Ecological Society of America.

Survival of *B. terrestris* was higher in the invasive treatments in the presence of newts than in the absence, while survival of *O. septentrionalis* was lower in the presence of newts [18].

While interactions between organisms have potential to inhibit keystone species, as was shown in the study by Navarrete and Menge, additive interactions do exist [14]. The brown bear, *Ursos arctos*, and the Pacific salmon, *Oncorhynchus* species, together serve as keystone species in the Pacific Northwest [19]. While most studies focus on the keystone effects of one species, keystone effects can result from the interaction between two or more species [19]. In the case of the brown bear and Pacific salmon, these keystone species interact together to transfer vital nutrients from the ocean to riparian habitat and rivers [19]. The essential cycling of nitrogen through these ecosystems is facilitated by these keystone species. The salmon carry nutrients from the ocean to the freshwater streams, where they spawn and die [19]. Their decaying carcasses provide essential nutrients to the riparian zones, after they have been removed from the water or hunted by bears; bear waste containing salmon also contribute to the enrichment [19]. The river and riparian ecosystems are thus fueled by the keystone interactions of the salmon and bear, illustrating the additive interactive effects of more than one keystone species on an ecosystem.

Habitat structure is a critical component to both terrestrial and aquatic ecosystems, providing organisms with opportunities to find and partition resources and seek refuge from predation [20]. As levels of structural complexity increase, diversity is hypothesized to increase; several studies have found elevated species richness and densities in freshwater and marine habitats as they have become more complex [21]. Beck discovered that total densities of gastropods were significantly greater in highly complex habitats versus those of lower complexity [22]. It seems probable that habitat complexity is capable of shaping keystone interactions; studies have demonstrated that foraging success of predators such as fish is hindered in more structurally complex habitats [15]. If increased habitat complexity provides organisms with greater refuge, it may

become more difficult for keystone predators to capture them. On the other hand, if there is a positive correlation between complexity and diversity, increased diversity may increase the chances of keystone interaction. Habitat heterogeneity is another factor that can impact diversity and species interactions [23]. It is also understood that the composition of species within a community can influence keystone interactions [4]. Though little research has directly investigated correlations between these factors and keystone interactions, it is highly likely that by changing levels of diversity, habitat complexity and heterogeneity are capable of directly or indirectly influencing keystone interactions.

It is clear that the strength of keystone effects on the community can potentially be influenced by interactions between the keystone species and other organisms, environmental factors, prey recruitment, and habitat qualities. While evidence suggests that keystone species can play a similar role in invaded communities, further research encompassing a wider variety of species and habitats, should be conducted. Even though the degree to which keystone species are influenced by abiotic and biotic factors can vary drastically, it can be said that a variety of factors will contribute to keystone interactions in any community. Regarding all keystone species research, wide ranges of species and habitats should be explored to see if patterns within one community can be found within others.

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