

## Opinion

## Humans as a Hyperkeystone Species

Boris Worm<sup>1,\*</sup> and Robert T. Paine<sup>2</sup>

Ecologists have identified numerous keystone species, defined as organisms that have outsized ecological impacts relative to their biomass. Here we identify human beings as a higher-order or ‘hyperkeystone’ species that drives complex interaction chains by affecting other keystone actors across different habitats. Strong indirect effects and a global reach further characterize these interactions and amplify the impacts of human activities on diverse ecosystems, from oceans to forests. We require better understanding of hyperkeystone interaction chains most urgently, especially for marine species and terrestrial large carnivores, which experience relatively higher exploitation rates than other species. This requires innovative approaches that integrate the study of human behavior with food-web theory, and which might provide surprising new insights into the complex ecology of our own species.

## A New Epoch for the Planet and for Ecology

There is now widespread acknowledgement that planet Earth has entered a novel geological epoch, the Anthropocene, which is functionally and stratigraphically distinct from the Holocene [1]. The Anthropocene is marked by the unprecedented effects of a single species, *Homo sapiens*, on the physical, chemical and biological makeup of our planet. The global reach of the human enterprise spreads these effects to all ecosystems, from the upper atmosphere to the deep sea. We suggest here that food webs provide a useful conceptual platform on which the ecological consequences of such environmental changes can be mapped, knowledge gaps identified, and predictions generated. In addition, food-web theory offers an understanding of the potentially complex interaction chains that might be generated by human interventions (Box 1). These interaction chains include both trophic effects mediated by direct exploitation and consumption, as well as non-trophic effects mediated for example by habitat alteration and pollution, competition and facilitation, or behavioral change.

As a prominent example of such theory, the keystone concept [2] has highlighted the disproportionate and often unexpected effects that a single species can have on food-web dynamics [3], biodiversity [4], and ecosystem functioning [5]. It has also revealed the importance of mechanistic knowledge about interaction chains that transmit keystone effects to other species. Such interaction chains can involve several species and trophic levels, and thus food-web theory can help to reveal complexities that might not be apparent otherwise (Box 1). Keystone species have previously been likened to the nodes in a power grid: when a single node is eliminated, the lights go out across different districts; this argument has also been used in conservation to motivate special protection for keystone species [6].

Keystones have been discovered in all major habitats, including grasslands, forests, freshwater, coastal, and open ocean communities [3,7]. The evidence comes from both experiments and observations (Figure 1A), as well as from food-web models (Figure 1B). What emerges from the available data is that carnivores are somewhat more likely to act as keystones in aquatic food

## Trends

Recent work highlights the unique ecology of our own species relative to other predators. For example, the median exploitation rates we exert on marine or terrestrial species are up to 15-fold higher than for any other predator.

We show that human exploitation as well as other impacts commonly affect known keystone species, driving potentially complex interaction chains that often remain unexplored.

We propose that such effects make humans a higher-order or ‘hyperkeystone’ species, which we define as a species that affects multiple other keystone species across habitats. While we focus on humans, it is likely that other far-ranging generalist predators, such as killer whales, could also be considered as hyperkeystone species.

Understanding our hyperkeystone role may require innovative approaches that merge observations, experiments, and food-web models, and will bring new insights into how our unique ecology is affecting global patterns of ecological change.

<sup>1</sup>Department of Biology, Dalhousie University, Halifax, NS B3H4R2, Canada

<sup>2</sup>Department of Biology, University of Washington, Seattle, WA 98195, USA

\*Correspondence: [bworm@dal.ca](mailto:bworm@dal.ca) (B. Worm).

## Box 1. Interaction Chains of Increasing Complexity

Human exploitation as well as non-trophic impacts can have complex effects on target and non-target species within and across interaction webs. Food-web theory can help us to understand, map, and manage these impacts. Arrows denote direct (solid lines) or indirect (dashed lines) effects, which can be positive (+) or negative (–). Shown are (i) direct effects of humans H on a target species A, (ii) direct and indirect effects on a target A and non-target species B linked through a trophic cascade, (iii) direct effect on a keystone species K with indirect effects on several non-target species B–E, and (iv) direct effects of humans on two keystone species operating in different interaction webs, with resulting indirect effects within and across food webs. Most natural resource management is focused on case (i), while variations in cases (ii) and (iii) have been described in the ecological literature. Potentially complex ‘hyperkeystone’ effects (iv) have received less attention, however. Not all possible indirect effects are shown (Figure 1).

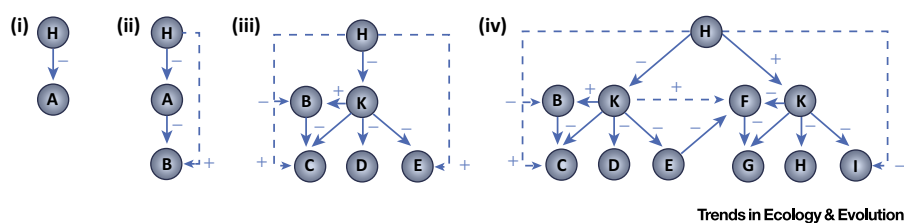


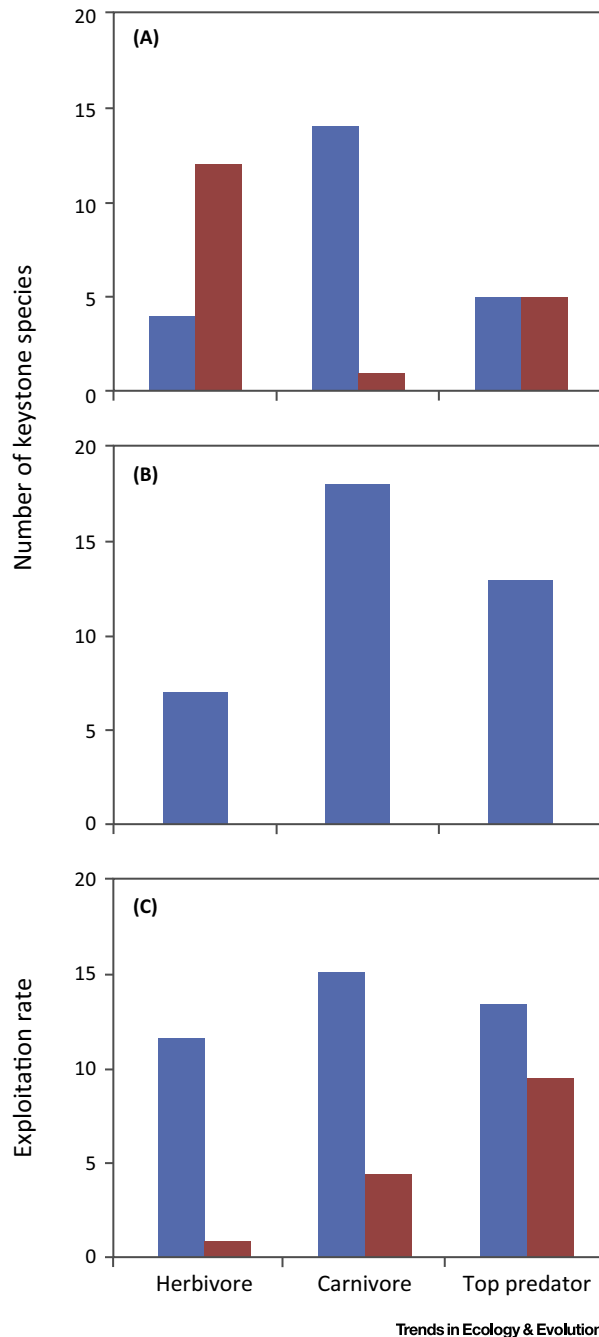
Figure 1. Direct Effects of Humans on Target Species and Possible Interaction Chains.

webs, whereas most documented keystone cases from land involve herbivores (Figure 1A,B). Note, however, that large carnivores are now rare in most land ecosystems, and hence their ecological roles might be underestimated; this is the classic ‘shifting baseline’ problem [8]. Many, if not most, of the documented keystone species are under direct human influence, for example through hunting and fishing (Figure 1C) but also through a host of non-trophic impacts [9–11]. While proximate population impacts on target species are often quantified, this does not tell us much about the wider consequences on ecosystems and their component species. What has been missing is a comprehensive evaluation of the complex interaction chains that can arise from the unique ecology of our own species [12]. Hence, the recognition of a novel geological epoch might also provide a new focus for ecology and the study of humans as a primary and dominant component of contemporary ecosystems.

### Understanding the Human Hyperkeystone Species

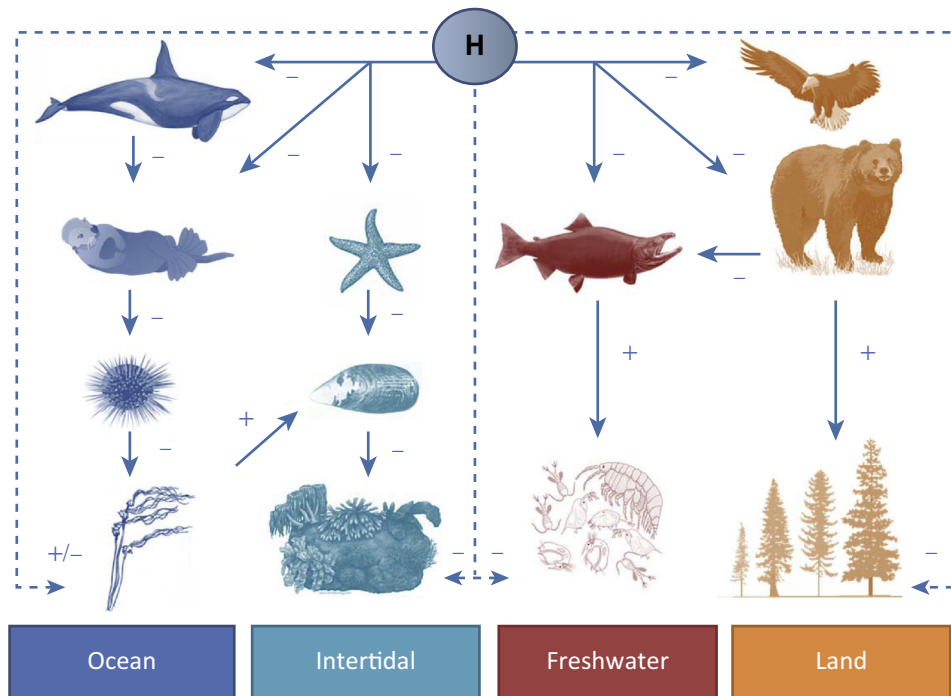
We feel that such a focus is timely because there is a growing and unprecedented interest in understanding the ecological role of our own species relative to that of other species. For example, a recent meta-analysis compared exploitation rates exerted by humans on their prey species to those of other predators [13,14]. It revealed that we exploit herbivores on land at a similar level to other predators (Figure 1C). By contrast, terrestrial carnivores and top predators are exploited by human hunters at median rates 4–10 times higher than other species; while in the marine realm exploitation rates by humans are 11–15 times greater than the median rate for other species (Figure 1C).

This is significant not only from a species-conservation perspective but also from an ecosystem. Many carnivores have been identified as keystone species (Figure 1A,B), and have been shown to control complex interaction chains [10,15,16] (Figure 2). By targeting these species at a substantially higher exploitation rate than others, we might deplete them to levels where their keystone role is compromised or lost. Their ecological role can remain vacant or sometimes be replaced by another species [17], and this could lead to novel interaction chains. In this way, humans are able to reorganize food webs by altering the position of traditional keystones. We propose that such a role makes humans a higher-order or ‘hyperkeystone’ species, a term we define akin to ‘hyperparasite’, as a species that affects multiple other keystone species across different habitats, and hence drives complex, potentially connected interaction chains (see Box 1 for a conceptual and Figure 2 for an empirical example).



**Figure 1. Keystone Species Across Different Habitats and Trophic Groups.** The number of herbivores, carnivores, and top predators that were identified as keystone species in (A) experiments and observations [3] and (B) food-web models [7]. (C) The median rate of exploitation that humans exert on herbivores, carnivores, and top predators, expressed relative to the median rate at which other predators exploit those species; data from [13,14]. Aquatic species are shown as blue bars and terrestrial species as brown bars.

Note that the impacts of humans on keystone species introduce indirect effects in all studied interaction chains, which affect basal species such as subtidal kelp, intertidal algae and invertebrates, stream invertebrates, and riparian forest trees in the Pacific Northwest (Figure 2). The mechanisms naturally differ: while the historic exploitation of sea otters has caused a classic



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**Figure 2. Humans as Hyperkeystone Species in the Pacific Northwest.** Depicted are known interactions chains that involve keystone species, such as orcas and otters [19], predatory starfish [2,20], and salmon, bears, and eagles [21,70]. ‘Hyperkeystone’ effects of humans (H) on those keystone species are mediated by the direct exploitation of otters [18] and salmon [71], the effects of historical whaling [22], fisheries [19], and noise [27] on orca foraging, climate-change effects on starfish [20], the effects of persistent pollutants on predatory birds [72,73], and the impacts of trophy hunting on bears and other large predators [13]. Positive interactions (+) include the provision of nutrient-rich detritus by kelp to filter feeders [5] and by spawning salmon to stream invertebrates and riparian forests [21,70]. Some selected indirect effects of humans on basal species are also shown (hatched lines). Note that interaction chains are linked across habitats, and about half of all interactions depicted are non-consumptive and are mitigated through other mechanisms.

trophic cascade to urchins and kelp [18,19], climate-change effects on predatory starfish transmit via predation on mussels and competitive interactions to intertidal algae and invertebrates [20] (Figure 2). In streams, salmon are recognized as a keystone species because they deposit marine-derived nutrients in upstream habitats; those nutrients are further deposited in riparian forests by bears and eagles [21] (Figure 2). While we focus on human hyperkeystone interactions here, we hypothesize that other far-ranging generalist predators, such as orcas for example, might upon closer study turn out to qualify as hyperkeystone species. This would amplify the wider consequences of changes in their distribution or abundance [19,22,23].

Clearly, the human hyperkeystone role is not new, but reaches back at least to the Pleistocene ‘overkill’ and resulting megafaunal collapse, which brought about novel vegetative states and altered fire regimes that profoundly changed landscape structure [24]. What is new is the planetary nature of our hyperkeystone role in a globalized economy, and the novel pathways by which these effects are being generated and transmitted. For example, anthropogenic noise, a relatively novel but increasingly ubiquitous form of human disturbance, can influence known keystone species through its effects on predator detection and perceived risk, for example in prairie dogs [25], or through its effects on foraging acoustics and stress levels in whales [26,27]. In both cases, however, the wider ecosystem effects of changes in prairie dog and whale

behavior have not been mapped out. The same is true for the potentially far-reaching effects of climate change [20] and ocean acidification [28] on keystone species: whereas immediate population-level effects are being actively investigated, the consequences for entire ecosystems often remain unexplored. Of course, interactions chains can also be affected by different human impacts at different levels. For example, in the classic predator–urchin–kelp chain, climate change can affect the kelp itself [29] and direct exploitation may target both predators and urchins [30], possibly disrupting this interaction chain altogether. Well-studied and tractable model systems such as rocky intertidal or subtidal communities offer key opportunities to map and understand the ecosystem consequences [31].

### Challenges and Opportunities in the Quest for (Hyper)Keystones

The study of the human hyperkeystone role requires an integration of the study of human behavior with the focused analysis of food-web mechanisms and processes. Nevertheless, in recent years many ecologists (including the first author) have shifted focus towards aggregate patterns of community structure, such as biomass and diversity, as well as their relation to aggregate functions such as productivity and nutrient cycling [32,33]. Macroecology has emerged as a dominant subfield, with a mandate to extract general patterns from the seemingly chaotic landscape of local biological variation [34,35]. A mechanistic focus on human-driven interaction chains and their dynamic behavior will be useful to complete the insights gained from such pattern-oriented analyses.

Humans have historically been treated as an externality, as if their effects belong in a separate category compared to other species and their interactions. This particular challenge was touched on 15 years ago by O'Neill and Kahn [12] who observed that ecologists treat humans as an externality while economists tend to treat ecosystems as an externality. Current approaches to study and manage coupled social-ecological systems attempt to bridge this gap [36], and would likely benefit from a new focus on keystone actors, both human and non-human. As an example we cite the rise of lobster population as a result of overfishing of their predators [37], which completely restructured both fishing communities and ecological communities in the Gulf of Maine, with interesting feedbacks between the two systems [38]. A striking terrestrial example concerned olive baboons in Ghana, which were released from apex predation as humans decimated their predators, and this indirectly impacted on crop production, child education, and human health [39]. These threads point towards a larger phenomenon: while we often have a reasonable understanding of the proximate effects of our most direct interactions on target species [13], the focus needs to be extended to capture complex interaction chains and their potential feedbacks on environmental quality and human well-being. The opportunity here is to reframe the ecological role of humans as a part of nature, not as a separate entity that can be studied in isolation.

Finally, an opportunity exists in treating the study of human impacts on food webs as quasi-experiments that enable us to learn more about nature itself and about the fundamental mechanisms that organize ecological communities. This is particularly useful in oceanic ecosystems that are not amenable to traditional experimental approaches [40]. The proven capacity of humans to alter community structure in these systems provides unique although often unappreciated pathways to understanding dynamics and testing ecological theory [41]. For example, May and colleagues [42] first modeled the indirect consequences of varied fishery management strategies in the krill-based South Polar ecosystem. Whale recovery can provide a probe of pelagic ecosystem organization, especially because whales can consume up to 62% of the net production of a system [43] and play a crucial role in nutrient cycling [44]. More recently, similar ideas have been explored in an effort to understand the general effects of removing low trophic level species, such as forage fish and invertebrates, on whole ecosystems [45,46]. The classic trophic cascade here is reversed because prey species are exploited and a wide variety

of predators are compromised [42,43]. Interestingly, some common rules emerge from these analyses, such as the observation that severe food-web effects can be mitigated by fishing forage fish at only half of the exploitation rate that would provide maximum yield [45]. Of course, such an 'experimentalist' perspective does not only apply to the extraction and depletion of species – similarly important insights might be gleaned from 'restoration experiments', as in the classic example of wolf reintroduction in Yellowstone National Park, which led to a wholly new understanding of herbivore and vegetation dynamics [47].

### Combining Approaches and Sharpening our Focus

Sharpening our focus on (hyper)keystone species will in our view require a creative combination of available tools and approaches, specifically long-term observation and careful manipulation of tractable communities [48,49], comparative experimental approaches across many sites [50], meta-analysis of observational datasets [51], and comparative food-web modeling [45]. The most convincing studies combine several of these approaches: for example, a now-classic study on the effects of large sharks on mesopredator and basal species off the US East Coast combined meta-analysis of fisheries monitoring time-series with experiments that manipulated mesopredator access to prey species, demonstrating an unsuspected interaction chain from sharks to shellfish [52]. Sharks similarly emerged as keystone actors in food-web models [7,53] and long-term observational datasets [23,48,54], leading to a more robust case overall. Because humans are exploiting sharks in all ecosystems where they occur [23], and at rates that often greatly exceed their reproductive capacity [55,56], a more general case can be made with respect to the human hyperkeystone role. Even so, aspects of the empirical data have been questioned [57]. Off the US East Coast, for example, the observed increase in mesopredator density in coastal areas proceeded more rapidly than predicted by life-history attributes [57]. We suggest here that non-trophic and behavioral effects, as well as changes in species distribution, might play additional roles [58,59]. Increased habitat use of mesopredators in 'fear-released' coastal systems might have augmented population increases driven by changes in mortality, and amplified the effects of mesopredators on coastal prey species. Clearly, combining the study of trophic and non-trophic effects is a current frontier in understanding complex interaction chains.

Integrating different analysis approaches and data sources seems generally necessary, especially where observed ecological change relates to human actions that are distant in either space or time [60]. We have alluded to the lasting impact of the Pleistocene 'overkill' above. Three further examples might illustrate the complexities involved in human interventions. Arctic foxes were introduced to some Aleutian islands for their valuable fur beginning in 1911, permitting these predators to decimate resident seabirds. The resultant islands with foxes present or absent permitted comparative studies that identified how marine nutrient subsidies delivered by seabirds linked two disparate ecosystems, changing a forb-dominated natural plant community to one dominated by grasses [61]. In a second example, Springer and van Vliet [62] have shown how the well-documented biannual life-cycle of pink salmon affects both zoo- and phytoplankton assemblage, which inversely influences productivity of plankton-feeding seabird colonies. Finally, it has been argued that intense post-World War II commercial whaling in the North Pacific ultimately led to a switch in orca diets that subsequently generated population declines in four other marine mammal species [22]. Some of the cascading effects extended from oceanic to nearshore ecosystems [19], but remain unexplored for three out of four affected marine mammal species. We argue that much will be gained by extending such interaction chains beyond their current membership to elucidate the behavior of humans as hyperkeystone species.

### The Urgency of an Expanded Perspective

There is an urgency to such an expanded perspective because an increasingly transnational human enterprise [63] is greatly magnifying our role as a hyperkeystone species [64]. A new perspective on human influence on ecological interaction chains should help to unify diverse

studies on changes in complex biological interactions (e.g., top-down trophic cascades [65] or the bottom-up effects of forage fish exploitation [45,46]), modifications to structural environments (e.g., ecosystem engineering [66]), and progressive changes to physical properties (e.g., global warming and ocean acidification [20,28]). This provides a strong argument that ecologists and conservation practitioners need to become increasingly aware of the importance of such connected interaction chains in driving ecological change across all different habitats [10,15,67,68].

How might a deeper understanding of the role of humans in contemporary ecosystems be achieved? Beyond the crucial issue of funding, and because not every species can be studied with equal effort, priority decisions must be made. These decisions must be based on direct or proxy knowledge of the role of a species, how that role is changing, and what the wider consequences of such change might be. Food-web models and meta-analyses of observational datasets can generate important insights, but detailed field observations, and controlled manipulations, will often provide the crucial evidence. Global modeling approaches focusing on dynamic food webs and their interactions [69] might ultimately provide a synthetic understanding of the novel ecosystem properties that arise from our global activities.

## Conclusions

We conclude that there is a need to more fully integrate the study of human of human behaviors and impacts with a deeper understanding of human-derived interaction chains and food-web processes. In this article we have focused mostly on one particular aspect of such interaction chains, as they relate to the keystone concept, and a human 'hyperkeystone role' that is characterized by far-reaching impacts on multiple keystone species across different habitats. We caution that this is of course only one aspect of the unique ecological role(s) that humans play in the Anthropocene, which needs to be complemented by other perspectives. Nevertheless, we feel convinced that the keystone concept, as it applies to human impacts on diverse foodwebs, will produce important insights into our unique ecology and collective place in nature.

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## Outstanding Questions

By which bottom-up or top-down pathways are humans affecting other keystone species?

How can we generalize from the many isolated case studies we have?

How are the resulting interaction chains connected?

What are the threshold densities below which a keystone species becomes functionally extinct?

Which other wide-ranging predators classify as hyperkeystone species?

How can we integrate insights from the study of individual interaction chains in global models?

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