A framework for the ELTONIAN niche of humans

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ABSTRACT

Recent research has highlighted several influential roles that humans play in ecosystems, including that of a super predator, hyperkeystone species, and niche constructor. This work has begun to describe the Eltonian niche of humans, which encompasses humanity's cumulative ecological and evolutionary roles in trophic systems. Yet, we lack a unifying framework that brings together these strands of research, links them to eco-evolutionary and social-cultural theory, and identifies current research needs. Here, we present such a framework in hope of facilitating a more holistic approach to operationalizing human roles in trophic systems across an increasingly anthropogenic biosphere. The framework underscores how humans play numerous nuanced roles in trophic systems, from top-down to bottom-up, that entail not only pernicious effects but also benefits for many nonhuman species. Such a nuanced view of the Eltonian niche of humans is important for understanding complex social-ecological system functioning and enacting effective policies and conservation measures.

KEYWORDS

Anthropocene; anthrome; community ecology; *Homo sapiens*; social-ecological systems

INTRODUCTION

Ostensibly, the study of ecology, which encompasses the relationships between organisms and their environments, should include humans within its purview, since *Homo sapiens* is a species that interacts with both biotic and abiotic components of ecosystems. Yet historically ecology has maintained a disciplinary tradition that has tended to place humans “outside” of ecosystems, or even of nature more broadly (Tansley 1935, Alberti et al. 2003). This dualistic view dominated the formative early years of ecology in Western societies (Tansley 1935, McDonnell and Pickett 1993). In the modern era, however, humanity’s local, regional, and global effects on ecosystems have begun to render such human-dominated versus “natural” dichotomies untenable (Alberti et al. 2003). Although humans have strongly influenced ecosystems for millennia (Jones 1969, Dunne et al. 2016, Trant et al. 2016, Fisher et al. 2019), the scale and magnitude of anthropogenic effects have soared in recent decades (Ellis 2011). As it has become increasingly clear that humans act as a dominant species across Earth’s ecosystems (Vitousek et al. 1997), ecologists have begun incorporating humans as a functional species into ecological thought and theory (McDonnell and Pickett 1993, Alberti et al. 2003, Dorresteijn et al. 2015, Dunne et al. 2016).

Only recently, however, have ecologists explored how humans act as an intrinsic, functional species within trophic systems. Hereafter, we use the term *trophic systems* in a general sense to refer to ecological communities consisting of more than one trophic level. Trophic systems are therefore inclusive of the classical ecological notion of *food webs* (cf. Polis and Winemiller 1995), but extend to include relationships beyond consumer-resource dynamics. Contemporary research has now documented how humans influence trophic systems in a variety of ways. For example, humans moderate the effects from apex predators by lethally exploiting them, modifying their behavior, and altering landscapes, and such effects can have cascading influence over broader trophic system dynamics in terrestrial and aquatic contexts alike (Ferretti et al. 2010, Estes et al. 2011, Ordiz et al. 2013, Oriol-Cotterill et al. 2015). Accordingly, humans have often been envisioned as affecting trophic systems from top-down positions (i.e., as an apex predator; Roopnarine 2014, Bugir et al. 2021). This top-down perspective has been reinforced by recent work classifying humans as *super predators* (i.e., a species that exploits another species at high rates or targets adult individuals with certain "trophy" characteristics; Darimont et al. 2015) and a *hyperkeystone species* (i.e., a high-order species that regulates other keystone species; Worm and Paine 2016).

However, humans should not only be envisioned to affect trophic systems through top-down pathways but also via those that are bottom-up. For instance, humans fix more atmospheric nitrogen than all other nonhuman sources combined (Vitousek et al. 1997), have caused the atmospheric carbon dioxide concentration to rise to a level that would be sustained for a millennium even if all human-related emissions immediately ceased (Solomon et al. 2009), and have transformed vast landscapes across the globe via agricultural practices and urbanization (Grimm et al. 2008, Pickett et al. 2011). In these and other ways, humans shape trophic systems by acting as a *niche constructor* that exerts intense selective pressure on nonhuman species via bottom-up pathways (Palumbi 2001, Smith 2007, Albuquerque et al. 2017). Moreover, humans not only shape trophic systems but also respond to them. Given that anthropogenic effects on such systems can feedback to affect human behavior, attitudes, and decision-making, humans must be viewed as an interactive agent that both affects and is affected by trophic system dynamics (Ostrom 2007; Box 1).

What is presently lacking is a unifying framework that brings together these strands of research and links them to eco-evolutionary theory and the social-cultural dimensions of human action and behavior. Here, we present such a framework by drawing upon the classical ecological concept of the *Eltonian niche*, which encompasses a species' functional roles within a given system (Sales et al. 2021, Elton 1927, Mittelbach 2012). Importantly, the Eltonian niche of modern humans is unlike that of nonhuman species in that it is more complex, multi-faceted, and system-dependent. As outlined above, humans should be expected to exert positive or negative direct influence on many – and perhaps all – species in a trophic system along multiple pathways, with complex indirect modifications to a variety of interactions between organisms. These human-triggered and multi-faceted effects can in turn alter system-level processes and feedback to influence human decision-making and behavior. Further, the intensities of such effects and their feedbacks vary considerably from system to system. For instance, North American and European hunters remove prey at rates roughly ten times that of their African counterparts, thereby acting as very different kinds of super predators, each with system-specific effects (Darimont et al. 2015). Given the potential for this complexity, ecologists must strive to take a multi-faceted approach to define the ecological roles of humans in a given system, operationalize them, analyze them systematically to determine their relative importance, and link the most salient anthropogenic effects stemming from these roles with policy and conservation efforts (Montgomery et al. 2018, 2020).

Below, we first describe a general Eltonian framework aimed at facilitating this goal and then we illustrate how it clarifies several prominent *Eltonian roles* humans play within trophic systems. To borrow classical terms from Hutchinson's definition of the niche (Hutchinson 1957), this effort can be viewed as first defining the fundamental Eltonian niche of humans writ large as all of the actions, roles, and trophic effects of humanity as a whole, and then highlighting several aspects of humans' realized Eltonian niche on a case- and system-specific basis (cf. Sales et al. 2021). We conclude by discussing the implications of our analysis for future research, conservation, and policy. We acknowledge that the concept of the niche has evolved over time and presently many different, occasionally conflicting, viewpoints are held (Sales et al. 2021). Here, we focus on the Eltonian concept, which emphasizes a species' role or "what it is doing" in a trophic system (Elton 1927). This focus is roughly analogous to the ecosystem ecology view as described by Chase and Liebold (2003) which emphasizes how species' functional traits impact systems rather than how environmental factors govern species' distributions (cf. Sales et al. 2021). Our focus also reflects the classical Hutchinsonian view that the niche is a property of a species rather than the environment (Hutchinson 1957). This species-centric aspect of the niche is especially pertinent to humans, as the functional ecological roles of humans have changed – and will continue to change – over time.

FRAMEWORK DESCRIPTION

At the highest and most general level, we structure the Eltonian framework of humans around five central, interconnected components (Fig. 1): *human decision-making* drives *human actions* that result in *ecological and evolutionary effects*. Human actions and their effects are characterized by several key *qualities*. Finally, the combination of human actions, ecological and evolutionary effects, and their qualities can lead to humans playing one or more of five unique *Eltonian roles* in a given system. Below we describe each of these components in turn.

At a fundamental level, *human decision-making* drives human actions and is responsive to reciprocal feedbacks emerging from the ecological and evolutionary effects of those actions (Fig. 2). Importantly, the cognitive capabilities and socio-cultural nature of humans are unlike any other species on Earth and translate to trophic effects that are not merely ecological in nature

(Manfredo 2008, Ellis 2015). We would be remiss not to mention that human actions are driven by normative attributes (e.g., values, attitudes, beliefs, interests, etc.) and social phenomena and processes (e.g., markets, governance, culture, etc.; Fig. 1), which are ultimately responsive to both ecological and non-ecological changes in social-ecological systems (Fulton et al. 1996, Manfredo 2008, Manfredo et al. 2014, Bennett et al. 2017). These drivers of human action are the subject of vast amounts of literature and research across disciplines beyond ecology, such as economics and philosophy, and thus fall outside the scope of this article. Nonetheless, drawing connections between ecological phenomena and the diverse socio-cultural drivers of human decision-making is crucial, and has given rise to interdisciplinary efforts such as the social-ecological systems framework (Ostrom 2007; Box 1). Although included in our framework, these drivers are not strictly a part of the Eltonian niche of humans, which is ecological in nature. Rather, they are the socio-cultural constructs and processes that give rise to particular realizations of the Eltonian niche of humans in a given system and location (Ellis 2015).

Thus, our framework focuses on the ecologically-relevant *human actions* that result from individual and collective human decision-making and their effects on trophic systems. We have organized these actions into four categories, including lethal exploitation (hunting, poaching, or culling), nonlethal activities (movement, travel, or recreation), landscape modification (infrastructure development, agricultural production, or activities associated with livestock), and translocation of nonhuman species (Fig. 2). This is because each of these actions have particular *ecological and evolutionary effects*. Ecological effects include direct effects on individual animals (e.g., via altered traits such as behavior) and populations (e.g., reductions, establishment, or persistence; Fig. 2). These direct effects can lead to indirect effects that can propagate through a trophic system vertically or horizontally, and can take any form of indirect effects described in classical ecological theory (Strauss 1991, Wootton 1994; Fig. 2), namely, exploitative competition (e.g., humans competing with marine predators for fish; Fig. 3a; Hansson et al. 2018), trophic cascades (e.g., humans lethally exploiting carnivores, thus benefiting their prey; Fig. 3b; Henke and Bryant 1999), apparent competition (e.g., human hunters targeting one species that leads to exploitation of a symatric species; Fig. 3c; Clayton et al. 1997), and indirect commensalisms and mutualisms (e.g., the "human shield" effect whereby humans benefit prey by repelling their predators; Fig. 3d; Hebblewhite et al. 2005, Berger 2007).

The aggregate consequences of direct and indirect effects are ecosystem-scale outcomes involving species' persistence, community dynamics, and ecosystem function and services (Fig. 2), which can result in singular, pulsed, or long-lasting changes to trophic systems (cf. Williams et al. 2020). For example, local, regulated hunting of wildlife species can result in pulsed compensatory mortality across seasons while altered soil chemistry due to agricultural practices can trigger rapid changes in microbial community structure that persist for many decades (Skalski et al. 2005, Fichtner et al. 2014). The intensity and temporal nature largely determine the evolutionary effects of these human-induced ecological dynamics. Finally, ecological outcomes related to both direct effects and their systems-level consequences feedback into human decision-making (Fig. 2; Box 1). For example, the ecosystem-level effects of apex carnivores include the regulation of nutrient cycles, hydrological dynamics, and community stability (Estes et al. 2011, Marshall et al. 2013, Ripple et al. 2014). These processes subsequently influence ecosystem services such as carbon storage (Schmitz et al. 2018). Thus, ecologically-focused human actions (e.g., reintroductions of these carnivores into systems where they have been extirpated) can have positive, trophic-mediated feedback effects on society, which in turn can influence human decision-making regarding land management, animal conservation, and carbon storage (Nelson et al. 2008, Schmitz et al. 2018). In such feedbacks, the lines between the ecology and sociology of humans become interactive. Much recent work in social-ecological systems has focused on understanding such connections, and the framework presented here serves to operationalize human-related roles in trophic systems from an ecological perspective (Box 1). Similarly, human actions can trigger direct and indirect ecological effects that feedback upon themselves (human-mediated ecological feedbacks; Fig. 2). For instance, in many areas across North America, white-tailed deer (*Odocoileus virginianus*) have become overabundant due to a lack of natural predators (DeYoung 2011). This species is a keystone herbivore that strongly influences vegetation structure and function through foraging pressure, and its overabundance can reduce plant diversity (Waller and Alverson 1997, Greenwald et al. 2008). Controlling white-tailed deer populations through lethal exploitation has been shown to not only effectively reduce their abundance (a direct effect), but also promote native plant biodiversity (an indirect effect) that in turn supports native bird communities (a human-mediated ecological feedback; McShea and Rappole 2000, Côté et al. 2004).

Human actions and their associated effects can be further characterized by three central *qualities*, namely their spatial scale (ranging from local to global), temporal nature (i.e., singular, occasional, pulsed, or continuous), and intensity (Fig. 2; see examples in Fig. 4). Often the qualities of human actions and their ecological effects will be tightly coupled. For example, more intense lethal exploitation of a given species is likely to have more intense ecological effects in the form of population decline (Packer et al. 2009, Fuller 2014, Darimont et al. 2015). Similarly, as human actions occur over larger spatial scales and become more continuous, their resultant ecological effects are likely to share these qualities. For instance, the burning of fossil fuels occurs near-continuously on a worldwide spatial scale, resulting in global ecological changes that will likely persist for millennia (Vitousek et al. 1997, Solomon et al. 2009). The intensity and scales of these ecological effects in turn drive evolutionary responses (Johnson and Munshi-South 2017, Des Roches et al. 2021). There are, of course, exceptions to these patterns. Low intensity, small scale, and singular human actions could have strong, large scale, and long-lasting ecological consequences, such as a single campfire igniting a large swath of prairie or forest (Balch et al. 2017). Likewise, high intensity human actions do not always translate to uniformly intense ecological or evolutionary effects. For example, the effects of herbicide applications can range from relatively innocuous to highly pernicious depending on the toxicity and environmental persistence of the chemical employed (Pratt et al. 1997, Newman 2014). Adding to these complexities are the non-linear changes that frequently occur in both human actions and their effects over time. For example, Native Americans in North America hunted the passenger pigeon (*Ectopistes migratorius*) at sustainable intensities for centuries, but European colonization and the hunting technologies that accompanied it non-linearly intensified and expanded hunting pressure to the point where the once-hyperabundant species was exterminated over several decades (Fuller 2014, Murray et al. 2017). Moreover, given the globalized nature of human economic activity and travel, local effects can be driven by human actions originating at vast distance. Such telecoupled relationships are common in social-ecological processes related to agriculture, ecotourism, commercial forestry, and exotic species translocation (Liu et al. 2007, 2013). Cataloguing all combinations of human actions, their effects, and their associated qualities is clearly beyond the scope of this paper (but see examples in Fig. 4). Nonetheless, the Eltonian framework presented here serves to help systematically identify these components so that they can be more effectively operationalized and examined for a given system or ecological issue (cf. Moll et al. 2019).

ELTONIAN ROLES PLAYED BY HUMANS

The Eltonian framework components described above provide context to clarify the nature of several prominent *Eltonian roles* that humans play in trophic systems and how they connect to the broader view of the Eltonian niche of humans. Stated another way, the broad components above define the fundamental Eltonian niche of humans in general terms that capture all the ways humans can function in trophic systems, while what follows focuses on the realized Eltonian niche of humans in particular cases (cf. Hutchinson 1957). Below we highlight three Eltonian roles that have been previously identified (super predators, hyperkeystone species, and niche constructors), and two which have been less formally articulated in the literature (pseudo-mutualists and risk-responders; Fig. 2).

Super predators

Humans can act as *super predators* when exploitative or nonlethal actions induce strong effects on species' populations or traits (Fig. 2). Notably, humans exploit wild animals at rates higher – sometimes much higher – than those documented among nonhuman species. In aquatic systems, for instance, humans exploit fish species at rates 14 times greater than those associated with nonhuman marine predators (Fig. 5a; Darimont et al., 2015). In terrestrial systems, human hunting of certain species can nearly double mortality from nonhuman predators (Darimont et al. 2015). Indeed, there are numerous examples of continent-wide defaunation events that exemplify humans' super predatory role over terrestrial fauna (Schwartz et al. 2003). Humans also function as super predators by removing predators and individuals that face virtually no threat from nonhuman predators. For example, unlike any other species, human hunters often target the healthiest and largest adult individuals or those possessing "trophy" characteristics (e.g., large antlers; Darimont et al. 2015). Note that the above super predatory rates calculated by Darimont et al. (2015) examined only the mortality of adults in prey populations rather than all individuals, further underscoring humans' unique focus on large, reproductively mature individuals. On broader timescales, both humans and related hominin ancestors have uniquely exerted strong top-down control over Earth's megafauna, leading to declines and extinctions of modern and historical species alike (Baker and Clapham 2004, Estes et al. 2011, Smith et al. 2018). Although unconstrained super predation typically leads to overexploitation and deleterious population-level effects (Darimont et al. 2009, 2015), humans' removal of adult individuals can also benefit ecosystems by controlling overabundant prey populations where nonhuman apex predators are absent (e.g., regulated hunting of herbivorous ungulates; McShea and Rappole 2000, Côté et al. 2004, Greenwald et al. 2008).

Initially, the term *super predators* focused on humans' lethal capabilities (Darimont et al. 2015). However, humans can also non-lethally alter species' behavior via the pathway of fear. A variety of species, from waterfowl to large ungulates, make behavioral adjustments to avoid encountering humans and vehicles (Frid and Dill 2002, Montgomery et al. 2020). These non-lethal risk effects even influence species situated in apex trophic positions (Clinchy et al. 2016, Smith et al. 2017, Montgomery et al. 2020). For example, many apex carnivores alter their spatio-temporal movement, activity, and foraging behavior to avoid humans, including pumas (*Puma concolor*; Smith et al. 2017; Fig. 5b), African lions (*Panthera leo*; Loveridge et al., 2017), brown bears (*Ursus arctos*; Ordiz et al., 2011), tigers (*Panthera tigris*; Carter et al., 2012) and Eurasian lynx (*Lynx lynx*; Gehr et al., 2017). Thus, humans function as super predators along lethal and nonlethal pathways. This role becomes increasingly prominent as lethal exploitation and nonlethal human activity grows more intense, spatially expansive, and continuous in nature (Darimont et al. 2015, Montgomery et al. 2020).

Hyperkeystone species

Humans can also play the role of a high-order *hyperkeystone species* when anthropogenic effects influence nonhuman keystone species, that is, those species whose trophic effects are disproportionately large to their abundance (Power et al. 1996, Worm and Paine 2016). Such cascading effects can result in dramatic consequences for ecosystem functioning, with the potential to restructure species assemblages and trophic system dynamics (Gill et al. 2009, Worm and Paine 2016). With respect to the broader Eltonian niche of humans (Fig. 2), this role can emerge any time that human actions begins to affect nonhuman keystone species in ways that modify the degree to which such species influence overall trophic dynamics. Examples of humans functioning as a hyperkeystone species include local extirpations of keystone species in both aquatic (e.g., sea otters *Enhydra lutis*; Estes and Palmisano 1974) and terrestrial systems (e.g., large carnivores; Fig. 5c; Darimont et al., 2015; Estes et al., 2011; Ripple et al., 2014). Such extirpations can release herbivore populations from predation pressure, triggering impacts that cascade down to vegetative communities (Estes et al. 2011). The hyperkeystone conception of humans as a functional species in trophic systems provides a bridge between research approaches focused on human behavior and those emphasizing classic food web theory (Worm and Paine 2016).

Niche constructor

A third Eltonian role humans can occupy is that of a *niche constructor* (Albuquerque et al., 2017; Ellis, 2015). Niche construction occurs when a species alters the environment in ways that initiate selective pressure inter- or intra-specifically (Odling-Smee 2003). Within this context, ecosystem engineering (Jones et al. 1994, Smith 2007) falls under the broader umbrella of niche construction (see Odling-Smee et al., 2013). In nonhuman species, classic examples of niche construction include the soil chemistry-altering effects of earthworms (Lee 1985) and “home construction” activities performed by numerous species (e.g., nest-building, burrowing, dam building; Odling-Smee et al., 2013). Humans are prolific niche constructors, with urbanization and animal domestication representing clear cases (Jones et al. 1994, Odling-Smee et al. 2013). In many instances, humans have created niches for species that in turn benefit society, a dynamic that has resulted in the coevolution of humans and agricultural crops and livestock (Ellis 2015).

Humans’ role as a niche constructor often results when landscape modification is intense and alters ecosystems through bottom-up pathways (Fig. 2; Box 2). For example, urban development replaces native habitat with artificial structures and landscaped vegetation, leading to a variety of effects on the species inhabiting a given system. In contexts with low basal resource levels (e.g., those in desert biomes), such urban development can translate to increased plant productivity and biodiversity due to water provisioning and landscaping (Faeth et al. 2005, Grimm et al. 2008, McKinney 2008), especially in wealthy areas of cities (i.e., a “luxury” effect; Hope et al. 2003). These changes can intensify bottom-up competition for resources by urban specialist species while reducing top-down pressures through the elimination of fragmentation-sensitive predators (Faeth et al. 2005). Urban areas in particular and landscape development more generally also elevate environmental noise and light to levels unprecedented in evolutionary time (Swaddle et al. 2015, Shannon et al. 2016). This anthropogenic sensory pollution alters selective pressures on a variety of ecological traits and processes, including physiology, mate selection, communication, and predator-prey interactions (Swaddle et al. 2015, Roca et al. 2016, Shannon et al. 2016; Fig. 5d). These pressures can drive rapid phenotypic changes over contemporary timescales (i.e., years to decades) and might result in eco-evolutionary feedbacks that impact ecosystem services and human health, although the potential for such dynamics are understudied (Francis et al. 2009, Alberti 2015, Swaddle et al. 2015, Alberti et al. 2017). On the whole, the acceleration of urbanization and other forms of landscape modification is resulting in a proliferation of emergent niches within evolutionarily novel “anthromes” across the planet (Ellis 2011). The spatial scales, temporal dynamics, and ecological characteristics of such anthromes vary considerably, but all are generally characterized by novel selective pressures driven by human actions that result in strong changes in eco-evolutionary dynamics and feedbacks (Ellis 2011, Alberti 2015, Miles et al. 2019).

Pseudo-mutualists

The roles above have been formalized in the literature and have tended to focus on the negative effects of humans on trophic systems. Such effects are certainly deserving of research attention. However, humans can also positively influence animal populations, and such positive influences can have reciprocal benefits for humans. Biocontrol efforts exemplify this phenomenon, whereby humans intentionally augment one species to control another that is considered undesirable from an anthropogenic perspective. For instance, human promotion of pest-controlling vertebrates (e.g., raptors) via nest box provision can benefit agricultural production by reducing seed and fruit predation (Lindell et al. 2018; Fig. 5e). Ecotourism is another example of how humans intentionally benefit species that are actively managed (e.g., via space and resource provision for species within a reserve) while receiving benefits in the form of pleasure derived from wildlife viewing and interaction (Skibins et al. 2012; Box 2). Consumptive human activities, such as hunting and fishing, are also often mutualistic when financial resources and enjoyment from recreation feedback to support the sustainable management of animal populations (Organ and Fritzell 2000, Granek et al. 2008). Finally, recent research has highlighted how human habitation, particularly by indigenous groups, over long periods (e.g., centuries to millennia) can enhance rather than degrade forest productivity and maintain a diverse mosaic of vegetation, often through the judicious application of fire (DeGraaf and Yamasaki 2001, Trant et al. 2016, Hoffman et al. 2017).

In the above and other instances, humans act as *pseudo-mutualists* that benefit other species while furthering human well-being. Notably, these beneficial human actions are often intentional and direct rather than mere incidental, auxiliary outcomes of human decision-making. In describing this role, the prefix *pseudo-* indicates that the benefits accrued to humans do not necessarily reflect the positive effects traditionally implied by mutualisms, such as enhanced fitness (Bronstein 2009). This, however, does not imply that such mutualism categorically fails to affect human fitness in the classic sense. For example, benefits accrued from wildlife in the form of psychological well-being improve human health (Miller 2005, Shanahan et al. 2016) and ecosystem services provided by numerous species (e.g., organic waste removal by scavengers; Whelan et al. 2008) likely have indirect effects on human life expectancy and population dynamics. However, studies on these human demographic responses are rare (Butler et al. 2005) and represent an intriguing line of future work.

Risk-responders

Humans are not only initiators of effects on trophic systems, but also recipients. For instance, humans regularly make behavioral decisions to avoid risks associated with perceived danger from non-human animals (Slovic and Peters 2006). Humans' evolutionary ancestors (i.e., species in the Primate order) exhibited a range of antipredator behaviors, including alarm calls, mobbing, and spatial avoidance (Gursky and Nekaris 2007). Similarly, humans' closest ancestors, Plio-Pleistocene hominins (6.0-1.8 Ma), mitigated predation risk from predators via vigilance, flight, and counterattack (Treves and Palmqvist 2007, Hart and Sussman 2009). These behaviors played a crucial role in hominid daily life in as recently as one million years ago (Hart and Sussman 2009).

Of course, most modern humans engage in lifestyles that are very different from those of our hominid ancestors. Nonetheless, evolutionarily-embedded antipredator behaviors linger in human consciousness, influencing individual and collective behavior (Hart and Sussman 2009), meaning humans can play the Eltonian role of *risk-responders*. For example, even though risk of injury from large carnivores is at a historic low, most people today still strongly express fear and intensify vigilance when presented with scenarios involving large carnivores (Jacobs et al. 2014). Humans also become more protective of household members (e.g., keeping children or pets indoors) when living in areas where carnivores are regularly encountered (Crooks and Soulé 1999, Collard 2012). Beyond such anti-predator responses, humans adjust behavior to avoid risk of discomfort or disease from many invertebrates and microbes (Curtis 2014). For example, Lyme disease, the most common vector-borne zoonotic in North America, is transmitted to humans via the bite of *Ixodes* ticks that carry an infectious bacterium (Nelson et al. 2015, Schwartz et al. 2017). Humans act as risk-responders and reduce exposure to ticks by changing their behavior, such as avoiding brushy areas that are favorable for ticks and reducing off-trail hiking during outdoor recreation (Fig. 5f; Center for Disease Control and Prevention 2020). Such altered behavior can reduce humans' ecological impact in forests and grasslands by spatially constraining human activity that would otherwise disturb animals and damage vegetation (Stankowich 2008, Barros and Pickering 2017).

Despite these behavioral responses to risk, the human role of a risk-responder has rarely been integrated into studies of human-trophic system interactions (Prokop and Fančovičová 2010). Doing so is crucial because the risk of negative interactions with nonhuman species not only influences human behavior (Killion et al. 2020), but also plays a role in shaping policy, conservation, and management by influencing human attitudes and values. For example, fear-inducing species, such as sharks or snakes, receive lower amounts of conservation support compared to neutral or aesthetically-pleasing species (Knight 2008, Liordos et al. 2017). Therefore, as in pseudo-mutualism, risk-responses entail feedbacks between humans and nonhuman species (Fig. 2). These feedback pathways can quickly become complex as the number of species related to a particular risk increase. For instance, although Lyme disease is transmitted to humans by ticks, as noted above, its overall prevalence is related to numerous abiotic and biotic ecological factors. One of these factors is the presence and abundance of certain mesocarnivores (e.g., foxes and mustelids), which are hypothesized to reduce Lyme disease via predation on the rodents that serve as a natural reservoir for the infectious bacteria (Levi et al. 2012, Hofmeester et al. 2017, Moll et al. 2020). Wildlife authorities typically allow for regulated harvest of such mesocarnivores. Recently, a citizen group petitioned for protection of these mesocarnivores with the aim of an indirect reduction of rodent populations and Lyme disease risk (Royar 2018). In this instance, one group's risk-response to ticks took the form of protecting other species in the trophic system, which created tension with a second group's value for harvesting those species. This example highlights how ecological and social values combine with complex trophic processes to create situations where humans play multiple Eltonian roles that can be in tension with one another, underscoring the need to take a social-ecological approach to finding resolutions for complex issues (Box 1).

IMPLICATIONS FOR FUTURE RESEARCH, CONSERVATION, AND POLICY

Ecologists are currently situated in a unique and somewhat perplexing position whereby virtually all systems under current study are strongly shaped by a species that has often been omitted from classical ecological theory and inquiry: humans (Tansley 1935, McDonnell and Pickett 1993). Today, this historical tendency is no longer defensible, and ecologists have increasingly sought to understand the myriad of ways that humans shape trophic systems (Alberti et al. 2003, Worm and Paine 2016). At the same time, social scientists studying human and natural systems have taken a broader approach to understand linked social and environmental outcomes (Ostrom 2007, Binder et al. 2013). The framework that we have developed here (Fig. 1, Fig. 2) provides a connection between these approaches unified under the classical ecological concept of the Eltonian niche.

Perhaps more than anything else, our analysis emphasizes how humans play numerous interconnected roles in trophic systems. As the above examples have shown, many ecologically- and evolutionarily-relevant human actions occur simultaneously, meaning that humans can play multiple influential Eltonian roles within a given system. An important first step to examine such complexity is to operationalize human actions by identifying their categorical classifications (i.e., lethal exploitation, landscape modification, nonlethal activity, and translocation) and characteristic qualities (i.e., their spatial scales, temporal nature, and intensity) within a given system (Box 2; Fig. 4). Such operationalization helps crystallize what is meant by the often-invoked but typically vague concept of "anthropogenic effects" (Moll et al. 2019, Montgomery et al. 2020). Humans' Eltonian roles vary between and within systems, and are propelled by diverse social and cultural forces that underlie human value systems and governance (Ellis 2015). We therefore discourage monolithic conceptualizations of modern humans as being a particular type of species, or as playing singular ecological roles. Casting the human species as predominately playing any one of the five roles discussed above – or any other singular ecological role – oversimplifies the manifold and context-specific ways in which humans affect trophic systems (Montgomery et al. 2020). Such oversimplifications undermine efforts to develop a clear understanding of the complexity of human-natural systems, which in turn hinders the development of effective policy and management for a given ecosystem (Liu et al. 2007, Montgomery et al. 2018).

Rather, we recommend that ecologists endeavor to capture the complexity of human effects in trophic systems by operationalizing multiple human-related variables in models and analyzing them systematically to determine which anthropogenic roles matter most in a given system (Dorresteijn et al. 2015, Dunne et al. 2016). Given that much research on human effects on trophic systems has focused on direct effects, there is a particularly pressing need to examine the extent to which such direct actions lead to indirect and system-level consequences (cf. Worm and Paine 2016) and resultant socio-eco-evolutionary dynamics (Des Roches et al. 2021). Importantly, multiple human-related variables should be integrated into broader interdisciplinary efforts that analyze social-ecological models by connecting humans' realized Eltonian niche to corresponding social drivers (Box 1). Certainly, efforts are currently being pursued towards these ends (Carter and Linnell 2016, Montgomery et al. 2018). One aim of our analysis is to make such endeavors more effective by organizing the manifold effects of humans on trophic systems in a coherent, ecologically-based framework.

Lastly, it is crucial to note that conservation policy and management will fail if they do not comprehensively account for the multifarious impacts humans have on trophic systems. For example, harvest management that only considers lethal effects of hunters while omitting their nonlethal effects on species' behavior will likely underestimate the overall impact of harvest regulations (Cromsigt et al. 2013). In contrast, policy that neglects the positive roles humans play in trophic systems will overestimate potential harm due to anthropogenic activity. For instance, policy aimed at bird conservation (e.g., the United States' Migratory Bird Treaty Act) must consider not only pernicious anthropogenic effects such as land conversion, but also human actions such as feeder provision that result in enormous benefits for many species (Davies et al. 2009). Therefore, the formation of effective policy and management requires taking a holistic view of the Eltonian niche of humans, cataloguing the roles played by humans in a given system, and identifying which of those are most prominent. Indeed, conservation policy has evolved over the last several decades from taking a species- and problem-specific approach to more holistic efforts focused on ecosystems (Nesshöver et al. 2017). We hope the framework presented here will advance these efforts by providing ecologists a common structure to account for human roles in trophic systems and a common language regarding these roles that can be shared by researchers, managers, policymakers, and conservation organizations.

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Box 1 Connections to social-ecological systems science

Humans and the environment are inherently connected. Several frameworks have been developed to address the various interactions, feedbacks, and complexities between these two systems (Pickett et al. 2005, Liu et al. 2007, Binder et al. 2013). Here we use the term social-ecological systems (SES) science to encompass this research. These paradigms position humans and the environment as interfacing parts of a larger, integrated, complex system to measure the effects of many multidirectional relationships. SES research relies on methodologies from diverse disciplines, where various epistemologies are applied to understand particular interactions between humans and the environment (Binder et al. 2013). For example, many SES approaches use social science theories to understand human decision-making processes in response to environmental changes (e.g., climate change adaptation, human-wildlife conflict, environmental hazard preparedness; Cote and Nightingale 2012). In these instances, traditional ecological models are paired with social data to simultaneously assess the effects of feedbacks between social and ecological units across spatial and temporal scales. Despite their promise, such approaches have been hindered by failing to adequately incorporate and operationalize ecological rules and theory (Rissman and Gillon 2017, Pulver et al. 2018)

Our ecologically-based evaluation of humans as a functional trophic species enhances a SES approach by clarifying how to operationalize humans' multifaceted effects on trophic processes as well as the feedbacks that emerge from such effects. Rather than reconstructing social processes as ecological ones, the roles described herein provide researchers with an ecological foundation to account for how humans interact with and impact trophic systems. For example, social surveys and interviews could be used to measure land owner attitudes and beliefs to estimate the probability of a land use decision, and the impact of that decision on local ungulate populations could be measured within an ecological framework using established principles (e.g., niche construction theory; Odling-Smee 2003, Smith 2007; Fig. 1). In this manner, the result of human behaviors is converted to ecological terms to better measure ecological effects, which forms a component of a larger SES analysis. Additionally, the framework can help operationalize the drivers of human behaviors, which are both ecological and social in nature. For example, an urban area with a nearby bear population might propose the use of secure garbage receptacles. The local community's acceptance of such a proposal could be analyzed using both ecological (e.g., human fear of physical harm) and socio-economic variables (e.g., a desire to protect property and belongings). In turn, the ecological effects of such a decision on bear behavior on lower trophic levels could be analyzed under the paradigm of anthropogenic niche construction. Thereby, such an analysis would evaluate the full feedback cycle of the ecological and social drivers of human decision-making as well as the trophic processes affected by those decisions.

Box 2 Applying the framework to contrasting systems

Although the framework can be applied to any trophic system, we illustrate its utility here by comparing the Eltonian niche of humans in contrasting systems: 1) that of a populous city with several hundred thousand inhabitants and 2) that of a large (i.e., thousands of km2) nature reserve or national park (hereafter *reserve*). Of course, specific realizations of such systems will vary according to many factors such as regional abiotic conditions and the socio-economic characteristics of states or nations. These differences notwithstanding, comparing humans' Eltonian niche across these prototypical systems helps clarify its context-dependence.

In the city, intense landscape modification will result in a heterogeneous mosaic of land covers ranging from city centers to greenways to less densely populated residential areas. The ecological consequences of these bottom-up trophic changes are manifold: connectivity and gene flow declines for most species but can increase for a select few well-adapted to fragmentation (Marzluff and Ewing 2001, Miles et al. 2018); overall biodiversity may be elevated compared to the city's surrounding area due to habitat heterogeneity, although non-native species will abound (McKinney 2002, Grimm et al. 2008, Parsons et al. 2018); lethal exploitation is typically highly regulated, limiting humans' super predatory role to particular species (e.g., pest species; Adams 2016); top predators are rare, resulting in increased bottom-up control of trophic dynamics (Faeth et al. 2005, Estes et al. 2011); resource availability is elevated and seasonally stabilized due to landscaping and water provisioning, which intensifies resource competition and favors generalists species tolerant of humans (Faeth et al. 2005, McKinney 2006). Additionally, nonlethal human activity in cities is very high, especially along transportation routes and areas of congregation such as commercial shopping centers. This activity triggers behavioral adaptations in wildlife (e.g., increased nocturnality; Gaynor et al. 2018, Moll et al. 2018), and vehicular traffic acts as a major source of animal mortality (Bateman and Fleming 2012) and a conduit for translocation events (Bullock et al. 2018). Thus, the predominant Eltonian role played by humans in this system is that of a niche constructor via intense and long-lasting landscape modification in the form of the built environment and the high-volume, daily-pulsed nonlethal human activity it supports (Pickett et al. 2011).

The Eltonian niche of humans in a large reserve differs markedly from that described above. Assuming effective regulation exists, lethal exploitation in the reserve is low overall but occasionally present and targeted (e.g., hunting a closely managed species; Wright et al. 2006). Landscape development is likewise relatively minimal, typically taking the form of road development, fencing, or waterhole provisioning (Valeix et al. 2009, Bojarska et al. 2017, Bull et al. 2018). Nonlethal human activity depends on recreation opportunity and interest, but is much lower than an urban context and exhibits temporal pulsing across tourist seasons (Newsome et al. 2012). Translocation events are infrequent but could be ecologically influential when exotic species are removed or keystone species are reintroduced (Hayward et al. 2007, Beschta and Ripple 2016). The gestalt ecological result of these collective actions is a relatively “intact” trophic structure where species interactions and food web dynamics more closely resemble those expected prior to human settlement of an area (although this will vary according to ecological and socio-cultural context; Jones 1969, Delcourt 2004). In contrast to the city, the predominant Eltonian role played by humans in such a reserve is that of a pseudo-mutualist via providing space for wildlife and plants that benefit of human well-being through the mechanisms of tourism, recreation, existence value, and ecosystem services.

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FIGURE CAPTIONS

Figure 1. A framework for the Eltonian niche of humans: *human decision-making* drives *human actions* that result in *ecological and evolutionary effects*. Human actions and their effects are characterized by several key *qualities*. The combination of human actions, ecological effects, and their qualities often lead to humans playing one or more of five predominant and unique *Eltonian roles* in a given system.

Figure 2. A detailed view of the Eltonian niche of humans. Arrows indicate causal processes. Eltonian roles (1-5) are special cases of broader categories in the framework, as follows: 1) *super predation* occurs when lethal exploitation or human-induced fear is of large magnitude, 2) landscape modification entails *niche construction* if resultant selective pressures persist across generations, 3) humans act as a *hyperkeystone* species when trophic effects are propagated via keystone species, 4) *risk-response* occurs when fear modifies human behavior, and 5) *pseudo-mutualism* occurs when humans benefit species that provides desirable services or value to humanity.

Figure 3. Incorporating humans into classic food web modules. Diagrams depict direct lethal and nonlethal effects (solid and double-lined arrows) and positive (+) and negative (-) indirect effects (dashed arrows). H = Human, C = Consumer Species, R = Resource Species. Panels: (a) human fishing of herring (*Clupea harengus*) results in exploitative competition with grey seals (*Halichoerus grypus*); (b) human exploitation of coyotes (*Canis latrans*) positively affects their prey, black-tailed jackrabbits (*Lepus californicus*); (c) apparent competition from human exploitation of sympatric ungulate species, white-tailed (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*); and (d) a human shield effect provides elk (*Cervus canadensis*) protection from human-averse wolves (*Canis lupus*). Images: Public Domain.

Figure 4. Examples of human actions across categories and qualities. In each colored graph, the spatial scale of the action increases vertically while intensity increases horizontally. The temporal nature of actions include singular or occasional, pulsed across various timescales, or relatively continuous. Colored arrows depict human actions that bridge categories.

Figure 5. Humans' Eltonian roles. Dashed arrows indicate effects that are behaviorally rather than numerically-mediated. Panels: (a) humans can act as super predators via lethal exploitation or (b) by inducing fear in apex predators (e.g., mountain lion *Puma concolor*); (c) humans can act as hyperkeystone species, as in gray wolf (*Canis lupus*) reintroduction into Yellowstone National Park, USA; (d) humans act as niche constructors by altering selective pressures via urbanization; (e) humans act as pseudo-mutualists by providing nest boxes for raptors that hunt agricultural pests; (f) humans act as risk-responders that avoid threatening species (e.g., the *Ixodes* ticks that act as a vector for Lyme disease). Images: Panel e – Florida Fish and Wildlife; others – Public Domain.