Evolutionary Ecology Research, **2023**: 103–117

Apparent competition: reflections on humans as mediators, agents, and victims of a pervasive indirect ecological (and sociological) interaction

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ABSTRACT

Objective: This essay honors the contribution of Michael Rosenzweig and his mentor Robert MacArthur to theoretical ecology by articulating how their intellectual contributions fed into my own, early-career conceptualization of apparent competition, an indirect interaction that can arise whenever alternative prey share predators with strong numerical and functional responses. The essay also pays homage to another dimension of Mike Rosenzweig's contributions—who has had a sustained concern with how humans engage with and one hopes sustains the natural environment (as in his 'reconciliation ecology')—by bringing out how apparent competition is a dimension in many human-generated conservation crises, and in human affairs.

Conclusions: Apparent competition plays a pervasive role in many conservation situations, because of introductions of species (predators or prey) and modifications of habitat, and because we humans ourselves can be devastating top predators, impacting scarce prey species to the point of extinction, precisely because our populations are sustained by alternative, productive resources. One can likewise discern apparent competition or comparable phenomena in many drivers of human history and suffering, ranging from spillover infections of pathogens from wildlife to ourselves, to interactions among different social groups. I suggest one reason to preserve biodiversity is because of its inherent intellectual value, which needs to be maintained for future generations. A clear understanding of drivers of extinction risk, such as apparent competition, is essential for this goal of preservation to be achieved.

Keywords: apparent competition, predation, humans as predators, humans as victims, introduced species, indirect interactions, isocline, value of biodiversity.

INTRODUCTION

This short note is in part crafted as a homage to Michael Rosenzweig (the founder of this journal) and his mentor Robert MacArthur. Mike recently told me in an email that his inspiration for one of his early, seminal papers (Rosenzweig and MacArthur, 1963) came from sitting in a lecture by MacArthur about competition, including the use of isoclines: "Robert introduced our freshman bio-1 class to the isocline method and I thought it was the coolest thing I'd ever seen. I was 18. And I was

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hooked. He'd done competition so I decided to tackle predation." How neat is that? He was stimulated to craft a paper that is still cited (according to Google Scholar over 100 times in 2021). Likewise, I was influenced by both MacArthur, my undergraduate advisor before he died in 1972, and Rosenzweig, whom I did not meet until later (in Jerusalem at INTECOL in 1978). I read Mike's papers avidly (including the one he wrote with MacArthur), as I thought through the theme of my first publication (Holt, 1977) back in graduate school. The term 'apparent competition' these days largely refers to negative indirect interactions between species because of a shared natural enemy that inflicts them both. One of the hallmarks of Mike's work on predation was his deft use of graphical isocline approaches, complemented with algebraic analyses (e.g., Rosenzweig, 1977). Inspired by his example, I likewise in that 1977 paper started with a consideration of qualitative insights gleaned from the shapes of predator isoclines. Mike's 1995 volume on species diversity provided a coherent perspective on the determinants of species diversity patterns, locally and around the globe. I do not think anything since matches up to the breadth of ideas about biodiversity Mike presented in this opus. If we want to maintain biodiversity, we certainly have to understand at a deep level the forces that maintain species coexistence and generate spatial and temporal patterns in diversity.

Unravelling the causal factors that drive human impacts on biodiversity is essential, if we are to mitigate those impacts. This paper is based on a talk I presented while visiting the Wissenschaftkolleg du Berlin on October 1, 2019 (blissfully unaware of the looming Covid tsunami), where the audience included many social scientists and humanists, not just natural scientists. This is the sort of audience for whom Mike's message of reconciliation ecology would have resonated. Many of the familiar themes of community ecology, ranging from exploitative competition, to trophic cascades, to ecosystem engineering, to competitive exclusion, are present and arguably important in determining human impacts on the natural world. Analogues of these ecological processes are pervasive within and among human societies, as well. In this paper, I will focus on apparent competition, involving humans in one way or another.

Humans are dietary generalists. We are omnivores consuming many taxa of animals and plants. There is growing evidence that through much of the history of *Homo sapiens*, it has played the role of a top generalist apex predator (Fleming and Ballard, 2017). There are also many instances in which humans have either introduced or eliminated species of both generalist predators and their prey, or influenced predator-prey interactions via habitat modification. The epigraph at the start of the extinction chapter in *Win-Win Ecology* (Rosenzweig, 2003) is a salient quote from Joseph Wood Krutch: "Of all living creatures man is the most dangerous—to everything else that lives as well as to himself." Many examples from applied ecology involve the indirect interaction of apparent competition between alternative prey species, mediated by a shared natural enemy (Holt, 1977; Holt and Bonsall, 2017), and in some cases, that shared enemy is ourselves. As the cartoon character Pogo Possum said, "We have met the enemy, and he is us."

I suggest that this indirect interaction pervades human impacts upon the natural environment, and that a recognition of this is needed to devise effective, clear-headed strategies for preserving biodiversity, and even for a deep understanding of our own history. Before dwelling on humans as agents, mediators—and even victims—of apparent competition, I provide some thoughts on why I think the preservation of biodiversity should matter in the first place.

WHY DO WE CARE ABOUT PRESERVING BIODIVERSITY?

No rational person can deny that *H. sapiens* has had a huge impact on biodiversity on the Earth, at both local and global scales, from early in the expansion of our species across the globe, to the present day (see chapter 11 in Rosenzweig, 2003). But why should we care? I do, deeply, but maybe that is a personal idiosyncrasy. Mike Rosenzweig also clearly cares, and for that reason he has championed how we can maintain species by modifying how we live in cohabitation with other creatures—the theme of "reconciliation ecology" (Rosenzweig, 2003). Scientists and philosophers have long grappled with the issue of why biodiversity should matter ethically. Some have contended that each species has an intrinsic right to existence. Ehrenfeld (1972: 5), for instance, states:

> The non-humanistic value of communities and species is the simplest of all to state: they should be conserved because they exist and because this existence is itself but the present expression of a continuing historical process of immense antiquity and majesty. Longstanding existence in Nature is deemed to carry with it the unimpeachable right to continued existence.

Other authors argue that it is difficult to ground this stance on firm philosophical principles. Newman et al. (2017: 396), for example, conclude after a book-length disquisition that, "At a bare minimum, the all-inclusive claim that 'biodiversity has intrinsic value' seems unlikely to be supportable." Along the way, Newman et al. (2017) consider what they call an aesthetic-value argument, which has to do with the value of conserving species or environments because of their "beauty"—a value which we project upon the entities in question. There is a kind of aesthetic value, however, which these authors do not consider, which is more abstract and intellectual, which provides a compelling value for the preservation of biodiversity. John Keats in his famed "Ode on a Grecian Urn" wrote, "Beauty is truth, truth beauty." Learning the "truth" about the world provides a kind of beauty that we can appreciate with our mind's eye, and that truth is very reticulate, and species- and environment-specific.

There is a value in preserving each species, when we can, because the loss of species is like burning books in the library of life (paraphrasing a famed quote from the US House Representative, John Dingell, "Living wild species are like a library of books still unread. Our heedless destruction of them is akin to burning that library without ever having read its books"). Each species has a unique "story" about itself and the world (Holt, 2009), written in its genome, its phenotype, and its suite of adaptations to particular environments. Barraclough defines "species" as follows: "a species [is] an independently evolving group of organisms that is genetically and phenotypically distinct from other such groups" (2019: 7). This "distinctiveness" is part of its "story." There is *an intrinsic, intellectual value in maintaining species*, and their environments (in which they have evolved, and to which they are adapted) regardless of pragmatic instrumental values such as bioprospecting windfalls and the like, because of the intellectual rewards derived from understanding the history, adaptations, and the peculiar quirks that almost all species have. As Ehrenfeld (1988: 215) says: "if more human-centered values are still deemed necessary, there are plenty available—for example, the value of the wonder, excitement, and challenge of so many species arising from a few dozen elements of the periodic table." The wanton loss of biodiversity caused by habitat modification and fragmentation, toxins, over-harvesting, and so forth, constitutes a huge intellectual loss to future generations.

There is also a looming, parallel loss of cultural diversity within our own species (Moseley and Nicolas 2010). For instance, around 40% of extant human languages are in danger of extinction (UNESCO, 2021). There are many reasons to lament this loss (Coen, 2020; Guvi, 2021). Eschner (2017) notes four such reasons: (1) we lose the expression of a unique vision of what it means to be human; (2) we lose memory of the planet's many histories and cultures; (3) we lose some of the best local resources for combatting environmental threats; and (4) some people lose their mother tongue. We think in words, and if you are the last speaker of a language, there is no one you can express those thoughts to, in exactly the way your mind frames them. The first three of these can be viewed as communal losses, in a sense, the last as an individual cost—a kind of ultimate loneliness. Each of these has parallels in terms of lines of reasoning as to why we might want to preserve biodiversity. When a species is lost, we lose both its "vision" (sculpted by natural selection and other evolutionary processes) as to what it means to be "alive" (#1), and also its record of its place in life's history (#2). Corresponding to (#3), one dimension of biodiversity is its potential role in food security. There are over 400,000 plant species (Enquist et al., 2019), many of which are edible, but humans consume only a few hundreds of these. And three species (maize, wheat, and rice) comprise an astonishing half of the calories and proteins humans consume (Warren, 2016). If a virulent mega-pathogen or egomaniacal despot came along that exterminated, say, wheat quickly, that would be—really, really bad. Hanging on to a diversity of alternative food sources is a kind of insurance policy, akin to the portfolio effect (Schindler et al., 2015). And I suspect bioprospecting has barely tapped what may potentially be present. Drescher et al. (2014) show that stingless bees benefit in the antimicrobial properties of their cuticle, if they can gather resin from a variety of plant sources. This corresponds to #3 of Eschner's list. There are analogues of #4 in biotic extinctions as well. One can listen online to a recording of the last male Kaui O'o, singing its heart out for a mate that will never come. It is heartbreaking.

APPARENT COMPETITION: A SHORT PERSONAL, HISTORICAL PERSPECTIVE

The interspecific interaction that has loomed largest in ecology is surely competition, which plays an equally large role in the social sciences. The Wikipedia definition of competition (January 10, 2021) is: "**Competition** is a rivalry where two or more parties strive for a common goal which cannot be shared: where one's gain is the other's loss." As just one of countless examples one could cite in human affairs, Stern (2019) reported impacts of mega-farms on Arizona residents: "In this *competition* for a scarce natural resource, those who can afford to drill the deepest wells are the ones who get the water, while those who can't are forced to abandon their property" (emphasis added). Adam Smith's "invisible hand" rests on self-interest and competition in a dynamic economy. Moudud (2021), in reflecting on the discipline of economics remarks: "Competition may be the spice of life, but in economics it has been more nearly the main dish. Competition has been a major force in the organization of production and the determination of prices and incomes: economic theory has accorded commensurate importance to the concept." Some scholars have argued that human history in large measure arises from competitive struggles between groups and nation-states. Peter Turchin (2017) remarks: "Warfare, and more generally, competition between societies, is one of the most powerful evolutionary forces explaining how human societies changed over the past 10,000 years" (and the conquering side often wins because it is subsidized by others). In *Ultrasociety* (2016), Turchin argues that human cooperation often reflects this history of competition—cooperation within groups is essential for effectively competing, among groups. All these usages of "competition" involve either direct interference, or indirect negative interactions caused by depleting a shared, limiting resource.

I suggest that the theme of my 1977 paper—apparent competition resulting from shared predation—is pertinent both to understanding how our species has impacted biodiversity, and to understanding the historical unfolding of our own societies. There are parallels to indirect ecological interactions with causal drivers in human social, political, and economic arrangements. I should caution that in many cases, the indirect interaction of apparent competition will just be one strand involved in a causal understanding of either ecological or socio-economic systems, which have many more interacting parts and chains of interactions than just alternative prey-sharing predators (or their human analogues). But for conceptual clarity, it is sometimes useful to leave aside those complexities and follow one strand, wherever it leads.

Back when I wrote that 1977 paper, the conventional wisdom seemed to be that predators tended to foster the maintenance of species diversity. Paine's famous and indeed beautiful experiments removing starfish predators from the intertidal zone of Tatoosh Island, Washington, leading to a collapse in intertidal community richness (Paine, 1966), led to a general impression that predators generically helped species to coexist. Keystone predators can indeed prevent monopolization of resources by any one prey species, thereby promoting diversity in the prey trophic level. There are human analogues of this ecological interaction. Governments, for instance, may have anti-monopoly laws, a top-down force that prevents monopolization of a particular economic sector by a single entity.

But already in the literature there was understanding that the impact of predators on diversity could be variable. In *Geographical Ecology* (1972), for instance, Robert MacArthur presciently noted this potential for heterogeneity in outcomes. On pages 192–194, he cited a study by Ruth Patrick (1970) in which consumption by a snail *Physa heterostropha* depressed diatom diversity, in part because the predator selectively ignored a common diatom species (*Cocconeis placentula*), which then grew to large numbers, presumably suppressing other species. Patrick, in that same paper, also noted that when stoneflies and caddisflies were present in a stream, they could keep in check numbers of blackflies, which otherwise would grow to great numbers and suppress other invertebrate populations. In this case, predation facilitates the maintenance of biodiversity. MacArthur discussed Paine's classic experiment, and remarked that predator "switching" (where predators behaviorally focus on whatever prey is relatively most abundant) could promote coexistence, as could specialist natural enemies (as in the Janzen-Connell effect). He also quite interestingly remarked that, ". . . these ceilings [one set by predators on total prey numbers, the other by competition among prey for resources] are usually interacting: the predator ceiling is lower where resources are scarce because consumers are ill fed and poorer at escaping, and the resource ceiling is lower where predation is severe because it is more dangerous to search for food." This intertwining of top-down and bottom-up effects has been a pervasive theme in ecology for many years (see chapter 11 in Mittelbach and McGill, 2019). There are surely parallels in socio-economic systems, such as the interplay of government regulation (a top-down force) and individual entrepreneurship (a bottom-up factor) in governing economic productivity. In conservation, implicit in Rosenzweig's "reconciliation ecology" is the interplay of top-down forces (e.g., establishment of large nature reserves) and bottom-up dynamics (people tending their own backyards to foster a diversity of other species).

MacArthur (1972: 21) provided the following definition of competition:

> . . . two species are competing if an increase in either one harms the other. Any machinery that can have that effect will be called competition. For instance, species A and B can fight, or A can reduce B's food supply, or A can, by its own losses, increase B's predators. Provided that the effect is reciprocal, we will call all three competition.

The first two have traditional names: interference competition and exploitative competition. There was no such name for the third possibility, which led me to coin the term "apparent competition" (alluding to the fact that most ecologists think of competition for resources when confronted with patterns consistent with competitive interactions). MacArthur (1965) earlier had remarked: "If . . . the different species of prey are so similar that the predators consume them in the proportion in which they occur, then that prey species which is least tolerant of predation will be eliminated." He went on to suggest that this could lead to limiting similarity among predator-limited species. My 1977 paper in a certain sense is an expanded exegesis of these crisp remarks by MacArthur.

Jane Lubchenco (1978) in a classic study showed that the impact of a natural enemy on diversity is context-dependent, even over fine spatial scales. The relationship between snail (*Littorina littorea*) abundance and algal diversity was hump-shaped in New England rock pools—a modest amount of herbivory facilitated species coexistence. However, a short distance away on rock faces, algal diversity declined monotonically with snail abundance. This is the same set of species, but presumably the correlation between consumer specificity and prey competitive ability shifts strongly between these two juxtaposed habitats. Jane was an assistant professor at Harvard, and I was at least dimly aware of this study during the 1970s, when I was mulling over studies such as Paine's, and it dawned on me that prey could interact indirectly via shared predators, just as exploitative competitors do via shared resources. In some cases (but not all), this could generate (–,–) interactions, potentially limiting community membership (e.g., by exclusion due to high predation, or aggravated extinction risk at low abundances).

Fast-forward to 2016, when I was invited to prepare a review of the apparent competition theme for *Annual Review of Ecology, Evolution, and Systematics*. The only prior extensive review was one with John Lawton in the same venue, several decades earlier (Holt and Lawton, 1994). I invited my friend Professor Mike Bonsall (Oxford University) to participate because of his own important experimental demonstrations of apparent competition in microcosms (e.g., Bonsall and Hassell, 1997). There were a large number of potentially relevant citations, and so we had a challenge in organizing this sprawling body of material. We decided to revisit the themes put forward in the 1977 piece, in effect walking through its outline, and asking what has happened since, and what completely new angles had emerged? We touched on, but did not dwell on, humans as either agents or victims of apparent competition.

The first step in Holt (1977) was to point out that an apparent competition effect was to be expected generically, across a wide range of ecological models. A simple, verbal argument is that if one finds that predation stably excludes a given focal prey species from a local community, there must be resident prey persisting with that predator, allowing it in turn to persist and act as a force of exclusion. Thus, those resident prey are indirectly culpable in the causal chain leading to exclusion of the focal prey. This argument is essentially independent of any details of predator-prey models.

Given that prey species do coexist, one needs to consider models in more detail. I devised a qualitative argument. If predators are food-limited (so their per capita growth rates depend solely on prey availability), then in a broad range of circumstances, alternative prey that coexist will suppress each other's densities. One can convince oneself of this conclusion by inspecting isocline shapes (see, e.g., figure 1 in Holt, 1977). My reading of Rosenzweig and MacArthur (1963) inspired me to think hard about what qualitative messages could be gleaned from pondering isocline shapes in the context of shared predation, and their example definitely entered into my producing this figure. I complemented this qualitative insight with a more detailed analysis of coexistence conditions in a model with logistic prey growth (but no direct interspecific competition), and a generalist predator with linear functional and numerical responses, with no direct density dependence in the predators. Each of these assumptions was then relaxed in that and later papers to examine the consequences of shared predation across a broad range of ecological possibilities.

In particular, if there is strong density dependence in the predator itself, and saturating functional responses, alternative prey species can experience indirect mutualism via a shared predator (comparing equilibrial abundances for each species when alone, versus together). An abrupt decline in the abundance of an alternative prey can lead to transient increases in predation upon a focal prey species, even if in the long run predator numbers decline leading to relaxed predation. An example involving barn owl predation upon an alcid and a deer mouse is described in Thomsen et al. (2018), and a theoretical exploration of such transient effects is provided by Serrouya et al. (2015).

HUMANS AS MEDIATORS OF APPARENT COMPETITION

Holt (1977) illustrated the idea of apparent competition by citing two plausible examples of habitat partitioning that were initially explained as due to resource competition, but later interpreted as reflecting shared predation. More recent compelling examples come from conservation biology. Humans can generate apparent competition by providing an alternative host for native generalist predators, which then can more intensively prey upon a given focal host species. Work by Gary Roemer and his colleagues on Santa Cruz Island has illuminated how apparent competition nearly drove to extinction the endemic Santa Cruz fox, a subspecies of *Urocyon littoralis* (Roemer et al., 2001; Roemer and Collins, 2020). Like many insular taxa, this species is relatively small; unlike their mainland ancestors, they are diurnal and not shy. The island was settled by ranchers in the 1850s. Their sheep overgrazed the native shrubby vegetation, producing non-native grasslands (Levy, 2010). The ranchers also introduced feral pigs, which became abundant, with around 5,000 adult pigs on a 25,000-ha island (about one pig per 5 ha—a very high density). These pigs then attracted golden eagles, who preyed on the piglets. The eagles, while attracted to the island from the mainland by the pigs, also found the foxes easy pickings. The foxes were dramatically declining until a feral-pig removal program was instituted—and then they rapidly recovered. This is a convincing example of apparent competition by feral pigs upon the endemic island fox. Such examples of apparent competition involving introduced species are now pervasive in the literature of conservation biology, invasion biology, and biological control. Feral pigs have been implicated in the extinction or endangerment of many taxa, worldwide (Risch et al., 2021). Impacts of invasive plant species on native plant communities can often be exerted via shared herbivores. Morris et al. (2017) describe how the invasive bush honeysuckle in the central United States exerts both short-term and long-term apparent competition on native plant species, via rodent and deer herbivory.

Sometimes humans introduce both the generalist predator and an alternative prey species that can sustain its numbers, allowing it to ravage native species. Courchamp et al. (1999), for instance, suggest that to control cat predation on island birds, one may need to simultaneously control introduced alternative prey, such as rabbits, not just the feline predator. In Australia, the introduced fox (*Vulpes vulpes*) and domestic cat (*Felis catus*) have particularly devastating impacts on native conilurine rodents wherever introduced rabbits (*Oryctolagus cuniculus*) are present (Smith and Quin, 1996). This issue of joint introductions leading to apparent competition arises frequently in biocontrol efforts. Louda et al. (1997) describe how the introduction of a biocontrol agent, the weevil *Rhinocyllus conicus*, introduced to control exotic thistles, also severely damaged a native thistle.

At times, human modulation of apparent competition can be indirect, for instance via modification of habitat structure. Serrouya et al. (2019) describe how forestry practices in western Canada increased the numbers of ungulate prey such as moose and white-tailed deer, which in turn increased wolf abundance. These wolves intensified predation upon woodland caribou (*Rangifer tarandus caribou*), risking their extirpation over large areas. Gradual reductions of alternative prey led to lower wolf numbers, and facilitated caribou persistence. (Rapid reductions in moose number can lead to transient pulses of heightened predation pressure, because individual predators shift foraging activities toward caribou.) Fryxell et al. (2020) sketch a similar argument for Ontario, suggesting that anthropogenic land-use change there has led to apparent competition harming woodland caribou via greater wolf predation. Solving this conservation problem requires one to deal with changing human land-use practices.

In all these examples, humans are mediators of apparent competition, either by introducing or eliminating other species, or by modifying habitats. In the remainder of this piece, I will focus first on humans themselves as the agent linking alternative species, leading to apparent competition between them, and then end with thoughts on how we can be victims of this indirect interaction.

HUMANS AS AGENTS OF APPARENT COMPETITION

As noted in Holt (1977), there were historical precedents for the idea of "apparent competition," albeit with only very brief mentions. The earliest example I have found is from Lotka (1925) who on page 95 states:

> A singularly interesting conclusion . . . of introducing a second prey species into a predator-prey interaction [which he represented in a model with exponential prey growth and constant attack rates] is that in . . . fisheries . . . [the] presence of a common fish may cause the extermination of a rarer species which, were it present alone, would be protected by its very scarcity, since this would make fishing unprofitable. But the more abundant fish continues to render a balance of profit from the trawling operations, and thus the rare species, so long as any of it remains, is gathered in with the same net that is cast primarily for common species.

There it is, the basic idea of apparent competition, 50 years earlier! As Ludwig Wittgenstein (1953/1968) remarked, "All progress looks bigger than it is" (translation from Kreisel, 1978). And, note that Lotka chose, as an example, *humans* as generalist predators. The predator "population" in question is the fishing fleet. The number of boats might wax and wane in accordance with the overall profitability of fishing operations. Moreover, if the entire fishing fleet is fixed in size, the number of boats working a particular locality could display an aggregative numerical response, which can lead to apparent competition among alternative fish species at that location (Holt and Kotler, 1987; Thurner et al., 2021).

Lotka's insight still haunts us today. At about the same time as I was crafting the 1977 paper, Colin Clark was exploring similar ideas in bioeconomics, with particular reference to the near-extinction of the great whales by human exploitation. Clark (1973: 632) notes: "Gulland [pers. comm.] has pointed out to me that fishing for the Antarctic blue whale probably would have become uneconomical several years earlier had it not been for the simultaneous occurrence of finback whales in the same area." Hunting for the finbacks permitted whaling fleets to remain profitable, yet high-value blue whales were captured whenever encountered. This permitted blue whales to be driven to very low densities, risking extinction, prior to the institution of international regulations protecting whales from exploitation (Clark, 2006). Branch et al. (2013) suggest that such "opportunistic exploitation" is pervasive in many industries that exploit living resources. Among the many examples they cite, in Zambia in the 1980s black rhinoceroses were poached to extinction, because poachers were making a living largely by hunting elephants—yet the poachers would kill rhinos whenever encountered. Likewise, in Sulawesi, snare hunters went after the abundant Sulawesi wild pig (*Sus celebensis*), but incidentally captured (and drove to low numbers) the much rarer babirusa (*Babyrousa celebensis*). Loggers have largely eradicated the valuable Madagascar rosewood (*Dalbergia* spp.) because other species of trees sustain the logging enterprise. The conservation implications of shared human exploitation are particularly serious when a sparse prey with low reproductive rates is preferred by a predator subsidized by many alternative sources of food or income (as in these examples, where the "predators" are whalers, poachers, and loggers).

When humans spread around the globe, colonizing the Americas, Australia, Madagascar, and other isolated areas, they were largely generalist carnivores (Ben-Dor et al., 2021). The arrival of humans was associated with waves of extinctions, particularly for mammalian and avian megafauna (Andermann et al., 2020). Alroy (2001) developed a simulation model, utilizing reasonable life-history parameters, attack rates, and other parameters, for both mammalian prey and the human population. He demonstrated that it was quite plausible that the extinction of megafaunal species was sustained by smaller-bodied, more fecund prey species. Broadly speaking, humans drove a "down-sizing" of mammalian faunas around the world, coincident with the increase in range and population size of humans (Smith et al., 2019). The authors suggest that these macroecological patterns are consistent with "the exploitation of mammals for food" during a phase in human history when we were largely carnivorous. Extirpation of large-bodied species would have been facilitated by the continued availability of smaller-bodied species. In other words, apparent competition with humans as the causal generalist predators leading to indirect interactions among mammalian taxa may have been responsible for molding the current structure of mammalian communities, worldwide. The extent to which human predation was directly responsible for the extinction of Pleistocene megafauna is still subject to debate (e.g., Broughton and Weitzel, 2018; Carotenuto et al., 2018), but the evidence does point to a substantial if not exclusive role. This implies one can point to the presence of alternative prey (which did not go extinct) permitting such over-exploitation as being indirectly causally implicated in these extinction waves.

Human-associated predation was greatly amplified when humans developed agriculture, boosting human population sizes. This, of course, led to large land-use changes which would impact many other species, regardless of exploitation. Yet although humans shifted lower in trophic rank in the overall composition of their diets, they did not become herbivores, exclusively. It is likely that human predation upon other taxa continued, but now with larger population sizes sustained by agricultural subsidies, there could be even more intense over-exploitation of targeted species. Large-bodied, flightless birds on islands were vulnerable to extinction by human exploitation (Fromm and Meiri, 2021). There is little reason, however, to believe that humans were ever totally dependent upon these particular prey for their subsistence, because the Polynesian and other indigenous peoples of Oceania carried agriculture with them as they settled these islands (Prebble et al., 2019). Certainly at present, humans are sustained largely by calories and nutrients derived from plants. The FAO (2022) estimates that just nine plant species comprise more than 75% of the calories sustaining our species. This "subsidy" (along with related livestock subsidies) permits us mercilessly to over-exploit many other taxa (as in the "bushmeat" trade found in tropical countries). Abstractly, this is a form of apparent competition, between domesticated plants and wild animal populations, mediated by human behavior (diet choice and habitat selection) and population size.

HUMANS AS VICTIMS OF APPARENT COMPETITION

The concluding, and more tentative, part of this essay has to do with how humans can at times be *victims* of apparent competition. Given that humans have largely escaped the ravages of predation ("lions, tigers, and bears"), this might seem to be an odd claim. Yet, much human suffering arises from infectious diseases and parasites that are harbored in natural mammal populations. To some degree, apparent competition is in play, whenever there is spillover infection from reservoir mammalian hosts to ourselves. Spillover among species is increasingly recognized as a significant source of disease epidemics (Power and Mitchell, 2004). For instance, Lyme disease is maintained by the complex interplay of tick, rodent, and deer dynamics. All these species—but not humans—are needed for completion of the life cycle of the causal agent of Lyme disease (the bacterium *Borrelia*) and its tick vector (Ostfeld, 2012). Incidental infection of humans via encounter with infected ticks causes considerable human suffering, and fluctuations in rodent host numbers (driving fluctuations in tick abundance), such as due to predation, can drive variation in human Lyme disease cases (Levi et al., 2012). This spillover infection into human victims can be viewed as a form of asymmetric apparent competition between rodents and humans. Note that this is distinct from the emergence of a novel infectious disease, which originated from a non-human reservoir host, but then spread via human-to-human infection processes. An example of the latter is the ongoing SARS-CoV-2 pandemic; the virus originated in an as yet unidentified Southeast Asian mammal, but its spread has been independent of that ancestral host species ever since. Haldane (1949) noted that parasites could be a potent weapon of competition. As Diamond (1997) famously argued in *Guns, Germs, and Steel*, human subpopulations carrying pathogens to which they are relatively immune, but to which other subpopulations are lethally vulnerable, have a powerful competitive advantage. Such asymmetric shared parasitism effects among human subpopulations have arguably facilitated European dominance in colonization of the New World and elsewhere (McNeil, 1976). Diamond moreover suggests that endemic tropical diseases such as malaria sustained by indigenous peoples prevented comparable European colonization of much of the tropical Old World. These historical drivers of human affairs can be viewed as a form of apparent competition, between alternative (human) host populations sharing a common pathogen.

As noted early in this essay, the theme of competition has been central to much thinking in the social sciences. Here, competition is not between humans and other species, but rather between different human entities (individuals, corporations, sports teams, nation-states, etc.). Could there be processes comparable to apparent competition within human affairs as well, leaving aside infectious disease? I think there likely are, but as I am not a social scientist, my thoughts here are necessarily rudimentary and a bit vague. For starters, one needs to identify human entities that play the role of "shared enemies" and "victims" required for apparent competition to arise in, say, a food web. The abundance or activity of the "enemy" would need to increase with the abundance or supply rate of the "victim." Many human interactions clearly involve exploitation of one group by another. Mehlum et al. (2006) identify a range of parasitic enterprises, ranging from "violent bandits and brutal mafia bosses [to] organized middlemen or smart political insiders," and Mehlum et al. (2000) develop a schematic mathematical model describing such parasitic, intraspecific exploitation. If the exploiters have multiple victim classes (e.g., the local Mafia extorts grocers, shoemakers, and banks), then those classes indirectly interact via the shared exploiter, leading to the potential for apparent competitive interactions among economic or social entities that might not compete in a traditional economic sense, at all.

At times, the analogue of predators may be a particular economic sector, rather than identifiable groups of individuals. Some economic theorists for instance have used analogues of Lotka-Volterra predator-prey models to examine how the rate of employment is related to the labor share of total income (e.g., Goodwin, 1967), or how the interaction between the "real" economy of the productive sector of the economy (manufacturing, agriculture, etc.) and the financial sector provides credit for non-output transactions (Dejuán and Dejuán-Bitriá, 2018). The latter authors argue this can generate bubbles followed by crashes, akin to predator-prey limit cycles; indeed, this can potentially generate chaotic dynamics (Goodwin, 1990). Turchin and Korotayev (2006) develop models analogous to predator-prey models to explore the relationship between internal warfare and population size. In all such models, if there is structure in the "prey" component of the system, akin to different prey species in an ecological community, then there is the potential for emergent negative indirect interactions between those structural elements.

Marxist economists, of course, view much of the modern capitalist economy as a form of parasitism, where workers are exploited for their surplus-labor. Keracher (1935), for instance, states that the "legal profession, insurance, advertising, and a host of other parasitic enterprises cling to the body of the real parasite—capitalism." Shelby (2002) refers to "Parasites, pimps and capitalists," a phrase which crisply encapsulates Marxist perspectives on capitalist economies. For non-Marxists, conversely, the privileged elites and ruling bureaucracies of officially Communist regimes have every appearance of being parasitic on the actual producers (peasants, factory workers, scientists, etc.). If the "hosts" or "prey" in these analyses have a substructure (e.g., different locations, social groups), they can indirectly interact via their shared "unnatural enemy." If one were to take this stance, literally, both modern capitalism and communism would likely be rife with analogues of apparent competition.

Empires by definition are geopolitical entities that straddle multiple local populations. It might be instructive to view the organization of empires in terms of indirect interactions among these populations. For instance, Crowhurst (2023) remarks about India in the British Empire in the nineteenth century:

> The contribution of India towards the British Empire in terms of providing essential raw materials, troops, and a pool of native labour prepared to go anywhere in the world was unsurpassed. It is possible to argue that most of the remaining colonies, excepting the dominions, cost much more than they gave the Empire, and Britain well could have done without them . . . By 1914 the British Empire extended over 24% of the world and included 23% of the world's population. That the British Empire was able to expand to the extent that it did would not have been possible without India.

Translating into ecological lingo, India was part of an asymmetric apparent competition interaction, sustaining an economy and military that could continue to subjugate swaths of the globe—akin to apparent competition, mediated by Britain's naval power and commercial maritime fleet.

In conclusion, I contend that apparent competition has been a pervasive feature of human impacts upon the natural world, and of humans upon themselves. Understanding this, I hope, might lead to improvements in applied ecology, and possibly help with interpreting our own history—relative to the rest of the biosphere—and each other. A clear understanding of the potentially complex causal drivers of extinction, including indirect interactions among species, is necessary for us to sustain what I above called the "intrinsic, intellectual value" of biodiversity for future generations to contemplate and cherish. This is necessary if we are to achieve the vision of Mike Rosenzweig (preamble to *Win-Win Ecology*, 2003):

There is still time. There is good reason to believe that civilization need not destroy most of the Earth's nonhuman species. The trick is to learn how to share spaces with other species . . . we can avoid a mass extinction of Earth's species without ourselves committing mass suicide.

The basic scientific insights that Mike has produced over his career, ranging from a deepened understanding of predator-prey interactions, to mechanisms of competitive coexistence in desert rodents, to habitat selection, to the spatial scaling of diversity, are all essential ingredients in ascertaining how best "to share spaces with other species." Thank you, Mike.

ACKNOWLEDGMENTS

I thank Douglas Morris and Sikander Khane for perceptive comments on the manuscript, Peter Turchin and Peter Crowhurst for valuable correspondence, Mike Barfield for many years of astute assistance in my research, Vitrell Sherif for editorial assistance, and the University of Florida Foundation for support. And, of course, Michael Rosenzweig for many years of intellectual inspiration and friendship.

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