



Research Letters

Human carnivory as a major driver of vertebrate extinction

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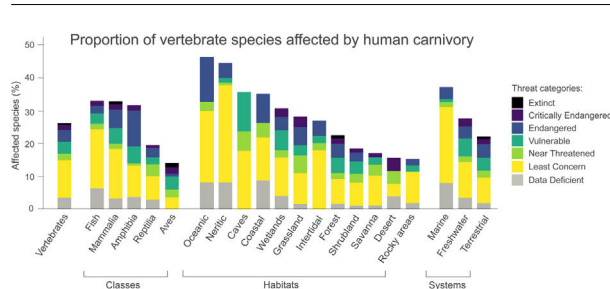
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HIGHLIGHTS

- Human carnivory threatens one-quarter of all vertebrates.
- This is a higher impact than that of other major aspects of human ecology.
- Human carnivory impacts wild vertebrates through multiple and ubiquitous mechanisms.
- Terrestrial and freshwater species are mainly affected by livestock production and predation.
- Aquatic species are mostly affected by predation and bycatch.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 14 December 2019
Accepted 9 October 2020
Available online 2 November 2020

Keywords:
Biodiversity crisis
Bycatch
Human ecology
Livestock
Predation
Trophic ecology

ABSTRACT

Although a considerable part of the anthropogenic impacts on other species has been caused by our habit of eating other animals, little attention has been given to understanding and quantifying how human carnivory threatens biodiversity globally. Herein we review the anthropogenic threats to 1000 species randomly selected among more than 46,000 vertebrate entries in the IUCN Red List database. We identified the following mechanisms by which human carnivory (i.e., our habit of feeding on other animals and related products) negatively affects the world's vertebrates: two mechanisms related to predation (predation and bycatch), two to competition (prey depletion and persecution), one to biohazards (any negative impacts caused by livestock or alien species whose introduction is linked to human carnivory), four to environmental changes (destructive harvesting practices, livestock, agriculture, and climate change), and a miscellaneous category for processes more indirectly connected with our high trophic position. Our conservative estimate, which does not include livestock impacts via agriculture and climate change, reveals that about one-quarter of the world's vertebrates are threatened by at least one mechanism related to human carnivory, and that this proportion is higher than that attributable to other leading causes of biodiversity decline including agriculture, forestry, infrastructure, pollution, invasive species, energy production and mining, fire regime and water systems modifications, and climate change. Our results suggest that human carnivory is the major driver of the current biodiversity crisis, and we hope our findings may contribute to raise awareness about this fundamental yet overlooked aspect of human ecology.

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Introduction

In the last few years, there has been a growing body of evidence that predation by humans has been at least a major cause of the worldwide extinction of many megafaunal species, such as woolly mammoths, hippo-like marsupials and giant sloths, along the last fifty thousand years (Sandom et al., 2014; Bartlett et al., 2015; Johnson et al., 2016; Surovell et al., 2016; Araujo et al., 2017). Marsupial lions, cave bears, and saber-tooth-tigers have also gone extinct around the same period, presumably not because of direct hunting, but because of prey scarcity and even direct competition with humans (Martin and Klein, 1984). Together, they form an astonishing collection that reminds us of the potential *Homo sapiens* has had to cause biodiversity loss, in both direct and indirect ways, through our predation on other animals.

As humans improved their technological repertoire and their populations exploded, the rate of species loss has skyrocketed to values comparable to those of the previous mass extinctions in the Earth's history. This implicates us as the drivers of the sixth mass extinction (Kolbert, 2014; Pimm et al., 2014; Ceballos et al., 2015), which is characterized by a huge increase of humans' and their livestock's biomass accompanied by a severe decline of wild vertebrates (Barnosky, 2008; Bar-On et al., 2018). Habitat alteration, overexploitation, invasive species, and climate change are the four major processes through which human activities have threatened the planet's biodiversity (Ducatez and Shine, 2017). Recently, the high environmental impacts of human carnivory – which we define here as our habit of eating other animals and related products – have increasingly indicated this aspect of human ecology as a key player in the current biodiversity crisis (e.g., Nijdam et al., 2012; Machovina et al., 2015; Ripple et al., 2015; Alexander et al., 2016; Davis et al., 2016; Frank et al., 2016; Clark and Tilman, 2017).

Human consumption of animal products (i.e., meat, other body parts, eggs, and dairy) certainly plays a critical role in those four processes through direct and indirect mechanisms. Agriculture is responsible for most land-use change and related environmental degradation worldwide (Foley et al., 2005, 2011). Approximately one-third of the calories produced by the world's crops is currently allocated to feed animals grown for human consumption, and when pasture and grazing lands are considered, livestock production accounts for approximately 70% of global agricultural land area (Steinfeld et al., 2006; Cassidy et al., 2013). Thus, the livestock sector is currently the single major driver of habitat loss and degradation, which is in its turn a leading cause of species decline and extinction worldwide (Viê et al., 2009; Ducatez and Shine, 2017). The production of livestock alters natural habitats not only via land-use change, but also through its outputs of agrochemicals, nutrients, sediments, antibiotics and hormones into natural environments (Steinfeld et al., 2006; FAO, 2018). Marine systems such as seagrass beds and coral reefs, which are among the most imperiled habitats on the planet, are severely affected by the pollution associated with land-use change (Islam and Tanaka, 2004; Camargo and Alonso, 2006; Diaz and Rosenberg, 2008). Moreover, livestock accounts for an estimated 43% of all water used in the global food system (Davis et al., 2016).

Concerning overexploitation of wild species, the impacts of human carnivory are not restricted to prehistoric times. Presently, the predatory behavior of humans has much stronger impacts on prey species than that of other top predators (Darimont et al., 2015), and overfishing and hunting for food are currently causing ecological extinctions and the severe decline of many species (Jackson et al., 2001; Ripple et al., 2016). Furthermore, animals domesticated for human consumption have been introduced outside their natural ranges across the globe. Confined livestock is known to impact native species through disease transmission (Garine-Wichatitsky et al., 2013; Krkošek, 2017), while free ranging and feral livestock

also prey upon native fauna and compete with it (Jolley et al., 2010; Ripple et al., 2015). Moreover, livestock-related genetic hazards are often a matter of concern, especially in the case of farmed fish species, which often escape into the wild (Laikre et al., 2010). These same detrimental interactions have been reported for wild animals introduced to habitats to which they are not native, in order to be later harvested for human consumption (Ogutu-Ohwayo, 1990; Bevins et al., 2014).

The release of carbon dioxide from land-use change and agricultural energy use, methane from enteric fermentation, and nitrous oxide from manure and fertilizer, makes the livestock sector responsible for an estimated 14.5% of the global anthropogenic greenhouse gases (GHGs) emissions (Gerber et al., 2013) – which is the same as the transportation sector (IPCC, 2014) – and for 74% of GHGs derived from the global food production system (Davis et al., 2016). Such emissions are a major cause of global climate change, one of the major threats to biodiversity. In addition to these mechanisms, many others such as bycatch (Lewison et al., 2014; Oliver et al., 2015), direct competition (Cury et al., 2011; Wolf and Ripple, 2016), retaliation against other predators (Inskip and Zimmermann, 2009), and killing animals such as dolphins and caimans to produce bait (Mangel et al., 2010; Brum et al., 2015) are ways by which human carnivory threatens wild vertebrate species.

The multiple, synergetic, and ubiquitous past and present processes by which human carnivory threatens the world's biodiversity makes it arguably the most detrimental aspect of our ecology, from a conservation point-of-view (Machovina et al., 2015). However, to our knowledge, there is no systematic review of such processes, and their impact on taxonomic and ecological groups remains overlooked. In this study, we offer a comprehensive review of the direct and indirect mechanisms by which human carnivory negatively affects the world's vertebrates. To give a more complete perspective of the impact of these mechanisms, the relative number of affected species are presented according to the taxonomic (classes) and ecological groups (habitats and systems) they belong to. We also estimate the proportion of vertebrate species that are threatened by at least one mechanism related to human carnivory, and compare this number with the proportion of species affected by other major aspects of human ecology.

Materials and methods

The IUCN Red List database presently includes 46,557 vertebrate species, distributed among the classes Myxini (the group comprising the hagfish), Cephalaspidomorphi (lampreys), Chondrichthyes (cartilaginous fish), Actinopterygii (ray-finned fish), Sarcopterygii (lobe-finned fish), Amphibia, Reptilia, Aves and Mammalia. In this study, we merged those five fish classes in a group including all fish species. To each species, a threat category is attributed; a species is considered threatened with extinction when it is classified as Vulnerable, Endangered, or Critically Endangered. The IUCN Red List database also provides information on population trends, and on the threats that affect assessed species in a categorical and descriptive way, given by the fields “threats list” and “threats” in the IUCN dataset, respectively (Table S1). The categorical threats follow the broadly used Unified Classification of Direct Threats created by the IUCN and the Conservation Measures Partnership (Salafsky et al., 2008). In addition to conservation-related information, each entry of the IUCN database also provides information on the habitats (e.g., forest, savanna, marine coastal) and systems (terrestrial, freshwater, marine) where each species occurs. A single species can be present in more than one habitat or system (Table S1).

Using a random data sampling without replacement in R environment, we selected 1000 vertebrate species among those 46,557 (Table S2). We then carefully read the fields “threats” and “threats

Table 1

Type, name and description of the identified mechanisms that negatively affect the world's vertebrates and are directly or indirectly caused by human carnivory. The term "livestock" includes domestic animals that have gone feral and hatchery fishes allowed to roam in the wild. Mechanisms marked with an * were not included in the quantitative analyses.

Type	Name	Description
Predation	Predation	Killing of wild animals for human consumption, including egg collection. Excludes the harvesting of wild animals for the following purposes: pet, cage bird, and aquarium trade; fur and feathers; bait; scientific research; traditional medicine; trophy hunting and recreational fishing.
	Bycatch	Unintentional killing of wild animals when attempting to kill other species of wild animals or feral livestock for human consumption. Includes fishing with poison and explosives if the assessed species is not threatened by predation.
Competition	Prey depletion	Depletion of prey species caused by competition with humans for the consumption of the same wild animal species.
	Persecution	Killing of wild animals to minimize competition for the same prey species or in retaliation to attacks to livestock. Includes persecution-related accidental deaths of non-target species.
Biohazards	Biohazards	Detrimental interactions with livestock and/or introduced species that were spread via fishery in the wild, hunting in the wild, aquaculture/mariculture, farmed animals, live food and live baits, contaminant nursery material, contaminant bait, and angling/fishing aquaculture equipment pathways. Excludes domestic dogs and cats and species introduced solely to be hunted for their fur.
Environmental changes	Destructive harvesting practices	Impacts on wild animals caused by habitat alterations from destructive hunting or fishing activities, such as hunting fires and blast fishing. Includes management of natural habitats for hunting and fishing purposes, such as suppressing some species' populations to increase the abundance of commercial or game species. Excludes trawling fishing.
	Livestock	Impacts on wild animals caused by habitat loss, destruction, degradation, conversion and fragmentation, water cycle changes, and pollution from livestock production or non-native species that were introduced to be harvested in the wild for human consumption. Includes habitat-related impacts such as grazing/herbivory/browsing, rooting/digging, trampling, and bio-fouling caused by animal species that were spread via fishery in the wild, hunting in the wild, aquaculture/mariculture, and farmed animals pathways.
	Agriculture*	Impacts on wild animals caused by habitat loss, destruction, degradation, conversion and fragmentation, water cycle change, and pollution from agricultural activities. Excludes forest regrowth after agricultural land abandonment.
Other	Climate change*	Impacts on wild animals caused by climate change.
	Other	Impacts on wild animals caused by other mechanisms that are attributable to human carnivory such as: killing of wild animals to be used as bait to catch target species for human consumption, killing of wild animals to be used as food for farmed animals to human consumption, and killing of wild animals by hunting dogs when accompanied by hunters. Includes impacts of trophic cascades caused by any mechanism related to human carnivory.

list" of those 1000 species, compiling the mechanisms related to human carnivory (Table 1) and identifying the species affected by each mechanism (Table S2). We compiled 10 mechanisms by which human carnivory affects the world's vertebrates: predation, bycatch, prey depletion, persecution, biohazards, destructive harvesting practices, livestock, agriculture, climate change, and other (Table 1). We designed this classification to intuitively convey the ecological meaning of the different impacts related to human carnivory. The agriculture and climate change mechanisms were not included in any quantitative analyses because the information in "threats" and "threats list" fields alone does not allow disentangling the cases where croplands and related impacts and climate change are driven by the production of livestock.

The identified mechanisms were considered to impact species independently of the threats' intensity, and independently of being related to past, present, or future threats. To avoid undue quantification of carnivory-related mechanisms, the information in the "threats" field was used as a complement to the information in the "threats list" field. For example, although *Pyrrhula murina* (line 203 in Table S2) is reported to be threatened by "hunting and trapping of terrestrial animals" in the field "threats list", we did not consider it to be threatened by human carnivory through the mechanism of predation because the "threats" field does not explicitly states this passerine bird is hunted for human consumption. When the "threats" and "threats list" fields did not provide unequivocal information about the purpose of "fishing and harvesting aquatic resources" threatening a fish species, this species was considered

to be affected by predation only if listed as of commercial interest in the FishBase (FishBase, 2019). To refine the detection of cases where human carnivory affects vertebrates through biohazards, we used the IUCN Global Database of Invasive Species (GDIS, 2019). We only considered biohazards those species whose introduction was directly or indirectly due to the human habit of feeding on other animals. Among all the pathways in the GDIS database, this criterion applies to species that were introduced via fishery in the wild, hunting in the wild, aquaculture/mariculture, farmed animals, live food and live bait, contaminant nursery material, contaminant bait, and angling/fishing aquaculture equipment (Table S3).

We recorded the proportion of species affected by each mechanism, according to taxonomic and ecological categories. The taxonomic categories include fishes (see above), amphibians, reptiles, birds, and mammals, while the ecological categories group species according to the habitats and systems they inhabit. We also estimated the proportion of vertebrates as a whole, as well as species within each taxonomic or ecological group, that are affected by at least one of the identified carnivory-related mechanisms (except agriculture and climate change). In all cases, the proportion of species within each threat category was also presented.

As a matter of comparison, we also estimated the proportion of vertebrates that are affected by the following aspects of human ecology: agriculture, forestry, infrastructure, pollution, invasive species, energy production and mining, fire regime and water systems modifications, and climate change. To do so, we used (1) the Unified Classification of Direct Threats (version 3.2) adopted by the

Table 2
 Number and proportion of species affected, affected and threatened with extinction, and affected with decreasing populations by major aspects of human ecology. These values are based on 1000 entries randomly selected from the 46,557 vertebrate species in the IUCN Red List's database. Proportions were calculated considering the 1000 sampled species, and the total number of species threatened with extinction (195) and with decreasing populations (253) within this sample. The direct threats included in each ecological aspect follow the Unified Classification of Direct Threats (version 3.2) adopted by the IUCN except for carnivory, which considers the mechanisms identified in the present study (except agriculture and climate change). Ecological aspects are ranked by the decreasing number of species they affect. *Includes all cropland area and related impacts, of which one-third are driven by the livestock sector through the production of animal feed (Steinfeld et al., 2006), as well as forestry effluents. **Includes agricultural effluents.

Ecological aspect	Description	Direct threats and respective codes	Affected		Affected threatened		Affected decreasing	
			Species number	Proportion (1000)	Species number	Proportion (195)	Species number	Proportion (253)
Carnivory	Human habit of feeding on other animals and related products.	Predation, bycatch, prey depletion, persecution, biohazards, destructive harvesting practices, livestock, and other.	261	26.1%	88	45.1%	100	39.5%
Agriculture*	Cropland and associated pollution and water use.	Annual and perennial non-timber crops (2.1), abstraction of surface water (agricultural use) (7.2.3), abstraction of ground water (agricultural use) (7.2.7), agricultural and forestry effluents (9.3).	261	26.1%	127	65.1%	137	54.2%
Forestry**	Pulpwood plantations, use of wild plant species, and associated pollution.	Wood and pulp plantations (2.2), gathering of terrestrial plants (5.2), logging and wood harvesting (5.3), agricultural and forestry effluents (9.3).	235	23.5%	115	59.0%	125	49.4%
Infrastructure	Human settlements and other non-agricultural land uses, transportation and service corridors, and associated pollution and water use.	Residential and commercial development (1), transportation and service corridors (4), abstraction of surface water (domestic use) (7.2.1), abstraction of surface water (commercial use) (7.2.2), abstraction of ground water (domestic use) (7.2.5), abstraction of ground water (commercial use) (7.2.6), domestic and urban waste water (9.1), garbage and solid waste (9.4), air-borne pollutants (9.5), light pollution (9.6.1), noise pollution (9.6.3).	172	17.2%	73	37.4%	90	35.6%

Table 2 (Continued)

Ecological aspect	Description	Direct threats and respective codes	Affected		Affected threatened		Affected decreasing	
			Species number	Proportion (1000)	Species number	Proportion (195)	Species number	Proportion (253)
Pollution	Introduction of exotic and/or excess materials or energy.	Domestic and urban waste water (9.1), industrial and military effluents (9.2), agricultural and forestry effluents (9.3), garbage and solid waste (9.4), air-borne pollutants (9.5), excess energy (9.6).	111	11.1%	53	27.2%	51	20.2%
Invasive species	Non-native and native plants, animals, pathogens/microbes, or genetic materials that have observed or predicted harmful effects on biodiversity following their introduction, spread and/or increase in abundance.	Invasive non-native/alien species/diseases (8.1), Problematic native species/diseases (8.2), introduced genetic material (8.3), problematic species/diseases of unknown origin (8.4), viral/prion-induced diseases (8.5), diseases of unknown origin (8.6).	104	10.4%	67	34.4%	57	22.5%
Fire regime and water systems modifications	Habitats conversion or degradation after managing of natural or semi-natural systems to improve human welfare.	Fire and fire suppression (7.1), dams and water management/use (7.2), other ecosystem modifications (7.3).	97	9.7%	52	26.7%	54	21.3%
Energy production and mining	Production of non-biological resources and associated water use and pollution.	Energy production and mining (3), small dams (7.2.9), large dams (7.2.10), dams (unknown size) (7.2.11), oil spills (9.2.1), seepage from mining (9.2.2), thermal pollution (9.6.2).	94	9.4%	46	23.6%	45	17.8%
Climate change	Long-term climatic changes which may be linked to global warming and other severe climatic/weather events that are outside the natural range of variation.	Habitat shifting and alteration (11.1), droughts (11.2), temperature extremes (11.3), storms and flooding (11.4), other impacts (11.5).	71	7.1%	33	16.9%	33	13.0%

IUCN to detect the threats associated with each one of these ecological aspects and (2) the field “threats list” of the IUCN sample to record the relative number of species affected by them (Table 2).

Results

Among the 1000 randomly selected species, we recognized two mechanisms related to predation (predation and bycatch), two to competition (prey depletion and persecution), one to biohazards, four to environmental changes (destructive harvesting practices, livestock, agriculture, and climate change), and other processes that are still ultimately caused by human carnivory but have more indirect connections with the mechanisms previously described. The mechanisms are described in Table 1.

When all sampled vertebrates are considered, predation affects the highest proportion of species (11.9%), followed by livestock (10.8%), bycatch (5.4%), and biohazards (3.3%) (Fig. 1a). For birds and mammals, predation and livestock are also the two most impacting mechanisms (Fig. 1e and f). For fishes, the role of livestock as the second most impacting mechanism is replaced by bycatch (Fig. 1b), while for amphibians and reptiles, livestock is by far the major menace (Fig. 1c and d). Biohazards have the highest impact in species that inhabit aquatic environments (Fig. 1b and c). With more than 20% of the species affected by a single mechanism, amphibians and mammals are the classes of vertebrates more severely affected by human carnivory, followed by fishes and reptiles ($\approx 18\%$). Livestock threatens 27.2%, 18% and 13.6% of amphibians, reptiles and mammals respectively, while predation affects 23.2% and 18.5% of mammals and fishes (Fig. 1).

It is worth noting that species threatened with extinction (i.e., those classified as Vulnerable, Endangered, or Critically Endangered) comprise a high proportion of affected species across many taxonomic and ecological groups (Figs. 1–3).

Vertebrates inhabiting terrestrial habitats, including inland wetlands, are mostly affected by livestock and predation, while marine species are primarily affected by predation and bycatch. More than 13% of vertebrates are affected by livestock in the majority of terrestrial habitats. Predation affects more than 20% of species inhabiting neritic, oceanic, and coastal/supratidal habitats, and bycatch affects more than 40% and 20% of oceanic and neritic dwellers, respectively. Competition-related mechanisms (prey depletion and persecution) also threaten more marine species than terrestrial ones. It is also worth highlighting the higher impact of biohazards in inland wetlands when compared to other habitats (Fig. 2).

A similar pattern is observed when vertebrates are grouped by system of occurrence. Human carnivory threatens the vertebrates inhabiting terrestrial and freshwater systems in similar ways, although the impact of predation and biohazards is higher on freshwater species when compared to terrestrial ones (Fig. 3a and b). As previously noted, marine species differ from those occurring in terrestrial and inland waters mainly because these species are primarily affected by bycatch and predation (Fig. 3c).

Human carnivory threatens 26.1% of the 1000 assessed vertebrate species through at least one of the following identified mechanisms: predation, bycatch, prey depletion, persecution, biohazards, destructive harvesting practices, livestock, and other. The most impacted taxonomic and ecological groups are fishes, mammals, amphibians, species that occur in oceanic, neritic and coastal marine habitats, caves and subterranean habitats, inland wetlands, and marine systems. Overall, aquatic species tend to be more affected by human carnivory than terrestrial species (Fig. 4).

Carnivory and agriculture (of which one-third of all cropland area and associated impacts are driven by the livestock sector) are the most impacting aspects of human ecology in terms of the proportion of vertebrate species they affect (26.1%), followed by

forestry (23.5%), infrastructure (17.2%), pollution (11.1%), and invasive species (10.4%) (Table 2).

Discussion

In this study, we identify the multiple mechanisms through which human carnivory threatens the world's vertebrates and we present the proportion of taxonomic and ecological groups impacted by these mechanisms. Our findings reveal that human carnivory threatens approximately one-quarter of the world's vertebrates and that this proportion is higher than that attributable to other major aspects of human ecology, suggesting that human carnivory might explain much of the global continuing decline of the world's vertebrates (Hoffmann et al., 2010; Tittensor et al., 2014).

Our quantitative analyses are based on 1000 randomly selected species among the 46,557 vertebrate entries comprised in the IUCN Red List. The IUCN database includes a high percentage of all described species of amphibians (84%), mammals (91%) and birds (100%). As these numbers have been considered sufficient to accurately estimate the percentage of threatened species within these taxa (IUCN, 2020), our results can be considered representative for these three groups of vertebrates. However, a bias in the representativeness of fishes and reptiles is likely to have occurred, as only 59% and 70% of all the described species are included in the same database (IUCN, 2020).

Because the IUCN database does not distinguish between the croplands that are used to produce plant-based food for people and for livestock, it is not possible to separate the species that are solely affected by these two ecologically different types of agriculture. This is why the mechanism agriculture was not included in the estimation of the impact of human carnivory on vertebrate species. However, as a high proportion of global crops are used as feed, not including agriculture in the list of mechanisms through which human carnivory threatens biodiversity would actually result in underestimating carnivory importance. The same rationale applies to climate change (Table 1). Therefore, our results are a conservative estimate of the impact of human carnivory on the world's vertebrates. This is especially true for the estimated number of species affected by at least one mechanism related to this aspect of human ecology (Fig. 4 and Table 2). Nonetheless, even considering that one-third of all cropland area and associated impacts included in agriculture actually corresponds to the production of livestock feed, we found that carnivory impacts the same proportion of vertebrate species (26.1%) as agriculture (Table 2). The IUCN database does not distinguish agricultural and forestry effluents either, which is another reason why the impacts of agriculture (and forestry) are overestimated (Table 2). For these reasons, we discuss the results shown in Table 2 considering human carnivory is indeed the ecological aspect of our species that most impacts the world's vertebrates.

Overall, livestock and predation were the mechanisms most affecting vertebrates that inhabit terrestrial and freshwater habitats and systems, while marine species are primarily threatened by predation and bycatch. The major role grazing and mowing play in habitat loss and degradation worldwide explains the high proportion of terrestrial and freshwater vertebrates we found to be threatened by the livestock mechanism. As threats to species occurring in habitats known to be highly impacted by livestock production (e.g., the Atlantic Forest of South America, Galindo-Leal and Câmara, 2003) are sometimes described as *lato sensu* agriculture in the IUCN database, these values are underestimated. Besides, according to the Unified Classification of Direct Threats, situations where a few animals mixed in a subsistence cropping system belong in “annual and perennial non-timber crops”, and foraging of wild resources for stall-fed animals falls under the threat “gathering

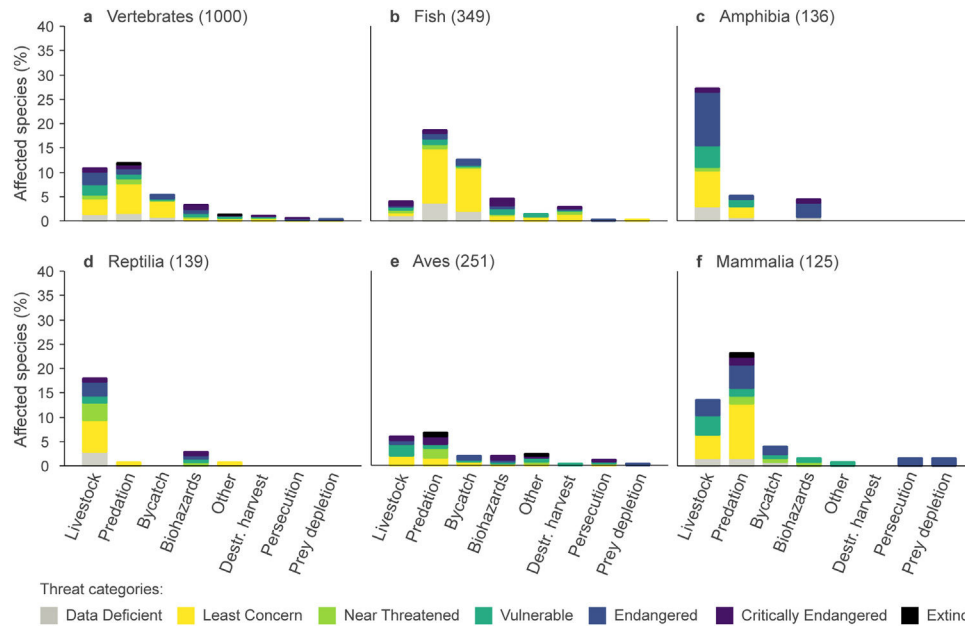


Fig. 1. Proportion of vertebrate taxonomic groups affected by the mechanisms related to human carnivory (predation, bycatch, prey depletion, persecution, biohazards, destructive harvesting practices, livestock, and other), distributed among the IUCN Red List's threat categories. The bars are not additive, as a single species may be threatened by more than one mechanism. These values are based on 1,000 entries randomly selected from the 46,557 vertebrate species in the IUCN database. The numbers in parentheses indicate the number of species assessed within each group. See Table S4 for detailed values.

terrestrial plants”, further contributing to underestimate the real impacts of livestock. Moreover, marine species inhabiting coastal and coral reef habitats, which comprise most fish diversity, are known to be severely affected by pollution associated with land-use change (Islam and Tanaka, 2004; Diaz and Rosenberg, 2008). However, as these threats are often included in the IUCN database under the general label of “agriculture and forestry effluents”, the proportion of marine species affected by the livestock mechanism is also underestimated, probably to a greater extent than terrestrial and freshwater species.

Wild caught fish is known to represent a major source of calories for human populations in the whole world, which explains the very high impact of predation on fish species. The even higher impact of this mechanism on mammals reinforces the dire threat bushmeat poses to this group (Ripple et al., 2016, 2019). Thus, the high proportion of species affected by predation reflects not only the exploitation of fish species but also terrestrial vertebrates for human consumption, especially mammals and, to a lesser but substantial extent, birds.

Bycatch was also very high for fish and marine species. Together with the impact of predation, this might explain the higher vulnerability of aquatic species to human carnivory when compared to terrestrial species (Fig. 4). As bycatch threatens a higher proportion of marine species than predation itself (Fig. 3c), our results confirm previous reports on the catastrophic unintended consequences of marine fisheries, both commercial and subsistence ones (Pauly et al., 1998; Jackson et al., 2001). Indeed, it has been conservatively estimated that 40.4% of all marine catches are discarded (Davies et al., 2009).

Biohazards include a variety of ways by which alien species that were introduced via pathways related to human carnivory interact with native vertebrates, such as predation, competition, hybridization, and disease transmission. Although these interactions could be separated into different mechanisms within the biological hazard type, we opted to lump them in a single mechanism because of the high frequency with which these interactions overlap in some taxa. For instance, it is common that introduced fish species negatively affect native species by predation, competition, and

hybridization, depending on the life stage of the assessed species. Moreover, the information in the threats field of the IUCN Red List often fails to detail what kind of interaction occurs between introduced and native species. Although biohazards impact vertebrate species to a lesser extent than livestock, predation and bycatch, it is important to note the relatively high impact this mechanism has on fishes, amphibians, and species inhabiting inland wetlands and grasslands.

Our results revealed competition-related mechanisms affect few vertebrate species when compared to other mechanisms. As the place of other vertebrate predators in the food chain is closer to that of humans, they are more prone to be affected by prey depletion and persecution than other species (Wolf and Ripple, 2016), and because they are naturally less numerous than herbivores, this mechanism is expected to have a less prominent impact when all vertebrates are considered. An analysis focusing on the impacts of human carnivory-related mechanisms on top predators would likely reveal competition as an important threat to these species. Indeed, prey scarcity and deliberate killing motivated by attacks to livestock and to reduce competition for the same prey species are a major concern to the conservation of wild carnivores worldwide (Donazar et al., 2005; Inskip and Zimmermann, 2009; Ripple et al., 2014). As the loss of top predators completely alters entire ecosystems in complex and unpredictable ways (Strong and Frank, 2010; Ripple et al., 2013; Atkins et al., 2019), competition and persecution mechanisms deserve more attention than our results suggest.

While trawling fishing is a harvesting practice that can be considered as destructive as blast and poison fishing, it was not included in the mechanism we called destructive harvesting practices, because the IUCN database frequently lacks information about whether trawling affects the assessed species through habitat destruction as well, in addition to predation and bycatch. A more detailed look at the ecology of marine vertebrates, especially bottom dwellers and those somehow dependent on reefs and sea prairies, would likely find a higher proportion of species affected by this mechanism, which is a major threat to some of the most sensitive and ecologically important habitats on the planet (Moberg and Folke, 1999; Orth et al., 2006).

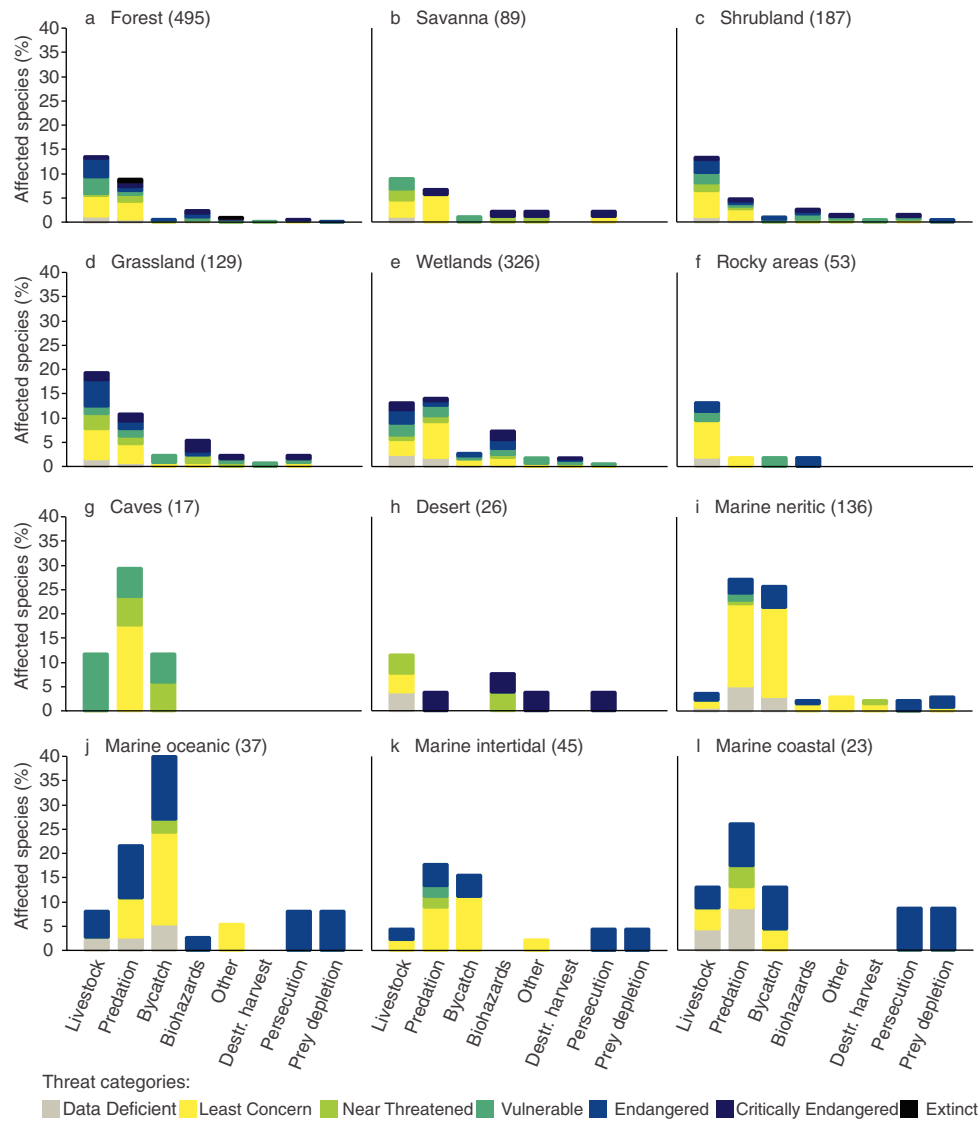


Fig. 2. Proportions of vertebrate species grouped by habitat of occurrence affected by the mechanisms related to human carnivory, distributed among the IUCN Red List's threat categories. Some species occur in more than one habitat. All the rest is like in Fig. 1. See Table S5 for detailed values.

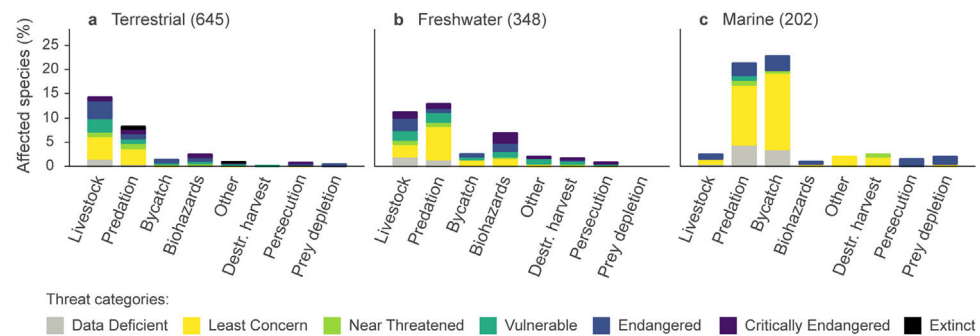


Fig. 3. Proportions of vertebrate species grouped by system of occurrence affected by the mechanisms related to human carnivory, distributed among the IUCN Red List's threat categories. Some species occur in more than one system. All the rest is like in Fig. 1. See Table S6 for detailed values.

Processes more indirectly related to the ones previously described were placed in the miscellaneous category. For example, the water bird *Phalaropus fulicarius* relies on predator alarm warning from another water bird *Sterna paradisaea*, whose populations have been reduced by egg collection for human consumption. Despite the importance of this kind of interactions between species,

these subtle processes frequently fail to be detected and reported as threats to the assessed taxa, especially those whose ecology is poorly known. This is also true concerning the ubiquitous impacts of trophic cascades, which occur far more often than acknowledged. Therefore, we believe the impact of mechanism “other” is also underestimated, and we call attention to the importance of

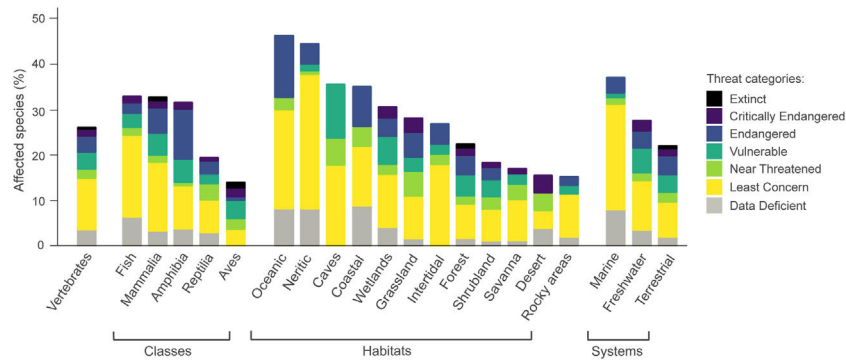


Fig. 4. Proportions of vertebrate species within taxonomic and ecological groups, and distributed among the IUCN Red List's threat categories, that are threatened by at least one of the following mechanisms related to human carnivory: predation, bycatch, prey depletion, persecution, biohazards, destructive harvesting practices, livestock, and other. These values are based on 1000 entries randomly selected from the 46,557 vertebrate species in the IUCN database. See Table S7 for detailed values.

including all the available information on species interactions in conservation assessments such as the IUCN Red List.

Final considerations

One of the main objectives of this article is to raise awareness about the real impact of human carnivory on biodiversity. Until recently, we have failed to recognize that our habit of eating other animals leads to several anthropogenic threats that greatly contribute to the current rates of species decline and extinction. This has prevented us from properly acknowledging the severity of the problem and finding practical solutions to mitigate it. The most important example is perhaps the case of agriculture. Assessments of the global food system's impacts have traditionally lumped under the general label "agriculture" the production of both plant-based and animal-based foods. However, due to the energy loss associated with higher trophic levels, the ecological impacts of animal products are fundamentally different in nature and severity when compared with the impacts associated with vegetal products. Indeed, recent studies have increasingly called attention to the importance of distinguishing between these two major types of food production (e.g. Graesser et al., 2015; Alexander et al., 2016). This situation also applies to other anthropogenic threats. For the purpose of creating public policies to preserve biodiversity, more useful than treating threats like prey depletion and retaliation against wild carnivores as problems of undefined origin, is to recognize the ultimate drivers behind them.

In brief, our conservative estimates (1) reveal that human carnivory threatens one-quarter of the world's vertebrates (mainly through the mechanisms of livestock production, predation, and bycatch), and (2) suggest that our habit of eating other animals and related products is, among other major aspects of human ecology, the one that most impacts biodiversity. Also, we highlight that competition-related mechanisms, as well as detrimental interactions with invasive species ultimately associated with human carnivory, are major overlooked threats for certain groups, such as carnivores and freshwater species, respectively. The numbers we present here advance our understanding on the enormous role human carnivory has on the ongoing biodiversity crisis found by previous studies (e.g., Machovina et al., 2015; Ripple et al., 2019), and reinforce the urgency to address this major yet overlooked aspect of human ecology. Our results support the growing idea that promoting a dietary shift toward plant-based diets is a promising strategy to halt the ongoing biodiversity crisis, and it should be a leading focus of global environmental policy (Machovina et al., 2015; Ripple et al., 2017).

While it is important to acknowledge the cultural and behavioral obstacles against the implementation of such a change, it is also true that opportunities do exist. This is because the consump-

tion of animal-based foods is not only linked with biodiversity loss, but also with other critical perils humanity currently faces, such as the global epidemic of non-communicable diseases, food and water security issues, and climate change. As a higher prevalence of obesity, diabetes, cardiovascular diseases, and some types of cancer are associated with the high and increasing consumption of animal products in both developed and emerging economies, public policies promoting a transition towards more plant-based diets have been increasingly recommended as a critical strategy to tackle the global non-communicable diseases health crisis (e.g. Tilman and Clark, 2014; Willett et al., 2019). While the consumption of animal-based foods is responsible for 43% and 87% of an individual's water and land-use footprint (respectively), these foods represent mere 18% and 39% of caloric and protein intake (Davis et al., 2016). This disproportionately high water and land requirements of animal-based foods compete with the production of crops that could be directly – and therefore more efficiently – used to feed people, generating a global concern about food and water security (Foley et al., 2011; Cassidy et al., 2013; Alexander et al., 2017). Finally, the very high contribution of animal-based foods' production to the global anthropogenic greenhouse gases emissions is yet another environmental dimension that confirms their inherent inefficiency. Not only the most impacting animal-based foods – like meat from ruminant animals (cattle, sheep, and goats) – are characterized by having an impact 20–100 times that of plant-based foods (Nijdam et al., 2012; Davis et al., 2016; Clark and Tilman, 2017), but even the lowest-impact animal products typically have higher environmental burdens than vegetal alternatives (Gephart et al., 2016; Clark and Tilman, 2017; Poore and Nemecek, 2018). Therefore, a transition towards plant-based diets also represents an opportunity to ameliorate climate change (Tilman and Clark, 2014; Springmann et al., 2018).

Practicable solutions to induce the substitution of animal-based foods by vegetal equivalents include: implementing fat, greenhouse gases and water taxes on meat and other animal products; eliminating subsidies to the livestock and fisheries sectors while providing adequate incentives to the supply chains of healthy foods; creating educational campaigns to inform the public about the health, social and environmental benefits of plant-based diets; and changing the available options in retail and food consumption settings (Steinfeld et al., 2006; Cassidy et al., 2013; Donati et al., 2016; Godfray et al., 2018).

If we are to halt the ongoing biodiversity crisis it is crucial to thoroughly identify the ultimate drivers of species' decline and extinction and to accurately quantify their impact. We hope our article convincingly conveys the urgent need to recognize that tackling human carnivory is a priority in any global strategy for biodiversity conservation.

Conflict of interest

None declared.

Acknowledgements

We thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) from the Brazilian Federal Government for providing a Ph.D. scholarship to Z.H. Coimbra; Guilherme Pontes for providing the vertebrate entries from the IUCN Red List database; Mariana Vale, Vinícius Farjalla and two anonymous reviewers for comments on early versions of the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.pecon.2020.10.002>.

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