

UNIVERSIDADE FEDERAL DO RIO DE JANEIRO
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA



ON THE ECOLOGY OF HUMAN CARNIVORY

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2019

UNIVERSIDADE FEDERAL DO RIO DE JANEIRO
CENTRO DE CIÊNCIAS DA SAÚDE
INSTITUTO DE BIOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

ON THE ECOLOGY OF HUMAN CARNIVORY

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Tese apresentada ao Programa de Pós-Graduação
em Ecologia da Universidade Federal do Rio de
Janeiro como parte dos requisitos para obtenção
do título de Doutora em Ecologia.

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RIO DE JANEIRO, RJ – BRASIL

ABRIL DE 2019



instituto de
biologia

UNIVERSIDADE
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RIO DE JANEIRO



Departamento de
ECOLOGIA

**ATA DA COMISSÃO EXAMINADORA DA TESE DE DOUTORADO EM ECOLOGIA
APRESENTADA E DEFENDIDA POR ZULMIRA HELENA GAMITO COIMBRA DE
ALMEIDA.**

No dia nove de maio de dois mil e dezenove, às quatorze horas, reuniu-se a Comissão Examinadora da Tese de Doutorado em Ecologia, apresentada e defendida por ZULMIRA HELENA GAMITO COIMBRA DE ALMEIDA intitulada: "On the ecology of human carnivory". A Comissão foi organizada obedecendo ao disposto nas Resoluções do Conselho de Ensino para Graduados e Pesquisa da UFRJ e no Regulamento do Curso de Pós-Graduação em Ecologia, estando constituída pelos membros: Dr(a). Fernando Antônio dos Santos Fernandez, Orientador (Presidente/UFRJ), Dr(a). Rafael Dias Loyola (UFG), Dr(a). Marcos de Souza Lima Figueiredo (UNIRIO), Dr(a). Ana Cristina Petry (UFRJ) e Dr(a). Vinicius Fortes Farjalla (UFRJ). Após o(a) candidato(a) apresentar sua tese tendo obedecido tempo estipulado no regulamento do PPGE, foi dada a palavra aos examinadores para arguição na seguinte ordem: Dr(a). Rafael Dias Loyola, Dr(a). Marcos de Souza Lima Figueiredo, Dr(a). Ana Cristina Petry, Dr(a). Vinicius Fortes Farjalla e Dr(a). Fernando Antônio dos Santos Fernandez, tendo o(a) candidato(a) respondido às perguntas formuladas. A seguir a Comissão examinadora reuniu-se para proceder ao julgamento, sendo atribuídos os seguintes conceitos: Dr(a). Rafael Dias Loyola, conceito A; Dr(a). Marcos de Souza Lima Figueiredo, conceito A; Dr(a). Ana Cristina Petry, conceito A; Dr(a). Vinicius Fortes Farjalla, conceito A; e Dr(a). Fernando Antônio dos Santos Fernandez, conceito A. Assim sendo, a Comissão Examinadora decidiu recomendar a outorga do Grau de Doutor em Ciências Biológicas (Ecologia) ao (à) candidato(a). Nada mais havendo a tratar, o Presidente da Comissão deu por encerrados os trabalhos e foi lavrada a presente ata, que vai devidamente assinada pelo Presidente e pelos Examinadores.

Rio de Janeiro, nove de maio de dois mil e dezenove.


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COIMBRA, Z.H.
On the ecology of human carnivory
[Rio de Janeiro] 2019
132 p. 29,7 cm (Instituto de Biologia/UFRJ, D.Sc., Ecologia, 2019)
Tese - Universidade Federal do Rio de Janeiro, PPGE
1. Nature conservation
2. Human development
3. Human ecology
4. Trophic ecology
5. Plant-based diets
I. IB/UFRJ II. Título (série)



To Olívia, the dearest white-eared opossum,
and to all non-human and human persons that somehow suffer
from the impacts of the global food system's greatest flaw.

But why does it matter what biases and emotional predispositions scientists bring to their studies – so long as they are scrupulously honest and other people with different proclivities check their results?

Carl Sagan in “The Demon-Haunted World”

ACKNOWLEDGMENTS

I would like to thank: Fernando Fernandez for accepting to be my advisor with a project on human ecology, for all the productive conversations, and for the careful revisions and pertinent comments to the three chapters of this thesis; Caio Kenup and Celso Gomes for their interest in the project, for their invaluable help in the analyses of chapters 1 (Celso), 2 and 3 (Caio), and for their precious suggestions and corrections to the same chapters; Guilherme Pontes for obtaining and organizing all vertebrates entries from the IUCN Red List database; Mariana Vale and Vinicius Farjalla for accompanying the development of my work and providing useful insights and corrections to early versions of chapters 1 and 2; Adrian Monjeau, Bernardo Araujo, Carlos Salvador, Carolina Starling, Catharina Kreischer, Diego Juffe-Bignoli, Filipa Palemirim, Hannah Ritchie, Júlia Niemeyer, Leandro Macedo, Manuel Eduardo dos Santos, Marcus Vieira and William Laurence for literature suggestions, comments, and answering questions; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for fellowship; all members of Laboratório de Ecologia e Conservação de Populações – UFRJ for the great work environment; André Lanna, Bernardo Araujo, Caio Kenup and João Lanna for hosting me in Rio de Janeiro; Everaldo Silva, Tina Reiter and Vanderlei Puhl for facilitating the access to the quiet places where I wrote most of this thesis; Celso Farneda for the much-appreciated logistic support; Helena Gamito for the enthusiastic incentive; and Fábio Farneda for all day-to-day support, for the great literature suggestions, and for encouraging me to develop the ideas I had along the process.

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ABSTRACT

It is well established that our species is responsible for the ongoing mass extinction, which started when *Homo sapiens* spread from Africa and exerted on other continent's fauna a hunting pressure heavier than large animals' populations were able to cope with. As human populations increased, so did their pressure on the ecosystems and the species inhabiting them. As a result, our activities currently threat the existence of even more resilient species. Although the long-term success of human populations depends on multiple ecosystem services delivered by natural environments, the development of our societies, which is essential to improve human well-being, is often considered incompatible with nature conservation. Human carnivory (i.e., our habit of feeding on other animals and related products), is arguably the single major driver of environmental degradation on the planet. However, the catastrophic consequences of this crucial aspect of human ecology on biodiversity and on the functioning of environmental services have been broadly overlooked. In this thesis (1) a systematic review of the direct and indirect mechanisms by which human carnivory threatens the world's vertebrates is presented, the impact of each one of those mechanisms on taxonomic and ecological groups of vertebrates is quantified, and the overall impact of human carnivory is compared with the impact of other major aspects of human ecology; (2) the correlation between natural environments and human well-being at country level is evaluated, and the Environmentally-adjusted Human Development Index (EHDI) is proposed; and (3) the agricultural area change in the world's countries under four scenarios of substitution of animal protein by vegetal protein is calculated,

as well as its expected effects on the EHDI. This thesis provides a novel and much useful tool to raise awareness among public policy makers and the general public about the disastrous ecological consequences of human carnivory to biodiversity and future generations. Furthermore, the results reveal the enormous potential of a shift towards plant-based diets to create remarkable opportunities for both nature conservation and long-term human development.

Keywords: biodiversity crisis, human development, human ecology, nature conservation, plant-based diets, trophic ecology.

RESUMO

É bem estabelecido que a nossa espécie é responsável pela decorrente extinção em massa, que começou quando o *Homo sapiens* saiu da África e exerceu sobre a fauna dos outros continentes uma pressão de caça mais forte do que aquela que as populações de animais de grande porte podiam suportar. À medida que as populações humanas aumentaram, aumentou também a sua pressão sobre os ecossistemas e as espécies que os habitam. Como resultado, as nossas atividades atualmente ameaçam a existência até de espécies mais resilientes. Apesar do sucesso a longo prazo das populações humanas depender de múltiplos serviços ecossistêmicos fornecidos pelos ambientes naturais, o desenvolvimento das nossas sociedades, que é essencial para melhorar o bem-estar humano, é frequentemente considerado incompatível com a conservação da natureza. A carnivoría humana (i.e., o nosso hábito de nos alimentarmos de outros animais e de produtos deles derivados), é argumentavelmente o principal impulsionador de degradação ambiental no planeta. Contudo, as consequências catastróficas deste aspecto crucial da ecologia humana para a biodiversidade e para o funcionamento dos serviços ecossistêmicos têm sido amplamente ignoradas. Nesta tese (1) é apresentada uma revisão sistemática dos mecanismos diretos e indiretos pelos quais a carnivoría humana ameaça as espécies de vertebrados do mundo, é quantificado o impacto de cada um desses mecanismos em grupos taxonômicos e ecológicos de vertebrados, e é comparado o impacto geral da carnivoría humana com o de outros principais aspectos da ecologia humana; (2) é avaliada a correlação entre ambientes naturais e o bem-estar humano ao nível de países, e é proposto o Índice de

Desenvolvimento Humano Ambientalmente Ajustado (IDHA); e (3) é calculada a mudança de área agrícola nos países do mundo sob quatro diferentes cenários de substituição de proteína de origem animal por proteína de origem vegetal, assim como o seu efeito no IDHA. Esta tese fornece uma ferramenta nova e útil para aumentar a conscientização de formuladores de políticas públicas e do público em geral sobre as desastrosas consequências ecológicas da carnivoría humana para a biodiversidade e as gerações futuras. Para além disso, os resultados revelam o enorme potencial de uma mudança para dietas à base de plantas para criar oportunidades notáveis de conservação da natureza e desenvolvimento humano a longo prazo.

Palavras-chave: conservação da natureza, crise de biodiversidade, desenvolvimento humano, dietas à base de plantas, ecologia humana, ecologia trófica.

GENERAL INTRODUCTION

For the first time in the Earth's history, a global mass extinction is being caused by a single species (Kolbert, 2014; Pimm *et al.*, 2014; Ceballos *et al.*, 2015). Due to its multiple ubiquitous and synergetic impacts on the ecosystems and the species inhabiting them, human carnivory, which is defined here by our habit of eating other animals and related products, is arguably the single major driver of the ongoing biodiversity crisis (Steinfeld *et al.*, 2006; Machovina *et al.*, 2015). In an ecosystem, the biomass retained in the bodies of primary consumers (herbivores) is 10% of the biomass of producers (plants), while the biomass of secondary and tertiary consumers (meso and large carnivores) is 10% of the biomass of primary and secondary consumers, respectively. This is the limiting principle that explains why large carnivores are naturally found in much lower numbers than organisms in lower trophic levels (Colinvaux 1980). It is thus not surprising that the sharp population increase of a primate species with an average weight of 67 kg and with an avid appetite for meat is associated with the staggering decline of wild vertebrates (Barnosky *et al.*, 2008; Bar-On *et al.*, 2018). This has happened not only because our ecology as predators is very similar to that of other top predators, and indeed more impacting (Darimont *et al.*, 2015), but also because as much as 36% of the terrestrial ice-free surface and 70% of global agricultural area is currently dedicated to feed the herds and flocks we have domesticated for our consumption (Steinfeld *et al.*, 2006; Erb *et al.*, 2016b). This numbers make the production of livestock by far the primary cause of land-use change and related environmental problems worldwide, which in its turns is a major cause of terrestrial species decline and extinction (Vié *et al.*, 2009;

Ducatez & Shine, 2016). It is evident that a large-bodied species like our own cannot be simultaneously abundant and have a high position in the food chain without causing profound ecological disruptions. However, we have failed to fully recognize this fundamental ecological rule and to include human carnivory as a focus of conservation biology, which has constrained the implementation of effective responses to the ongoing biodiversity crisis.

Our impact on the ecosystems and the species that inhabit them is proportional to the product of the size of our populations, the consumption per capita, and the technology at our grasp (Holdren & Ehrlich 1974). Currently, the planet is inhabited by approximately 7.7 billions of humans (United Nations, 2017). Population growth rate has steadily decreased in the majority of the world's countries during the last decades. The spontaneous reduction of fertility rates behind this phenomenon has been explained by a decrease of infant and child mortality, and an increase of urbanization, education, and income (Mace, 2008; Sachs, 2008; Mace *et al.*, 2013). However, increasing growth rates in some regions of the world (mainly Sub-Saharan Africa) and lower growth rates of already large populations make global population unlikely to stop growing this century (Gerland *et al.*, 2014). As even a rapid transition to a worldwide one-child policy would have modest results, human population stability and reduction will certainly not happen in time to solve current environmental problems (Bradshaw & Brook, 2014). Moreover, higher income levels are associated with both lower population growth rates and higher consumption levels per capita, to which the consumption of highly impacting animal products is no exception (Kearney, 2010; Tilman *et al.*, 2011; Kastner *et al.*, 2012; Weinzettel *et al.*, 2013). Therefore, further decreasing fertility rates in countries with more environmental impact per

capita, which is much more challenging than reducing fertility in fast growing populations, is not a cost-effective solution.

The intensification of agriculture has been suggested to cope with the increasing demand for food and animal products that is projected to occur in the coming decades without causing further conversion of natural habitats into pastures and croplands (Foley *et al.*, 2011; Tilman *et al.*, 2011). Although technological solutions can contribute to improve yields and reduce waste (Godfray & Garnett, 2014; Rööß *et al.*, 2017), they are insufficient to ensure the desired environmental and food security outcomes (Garnett *et al.*, 2013; Smith *et al.*, 2013; Davis *et al.*, 2016; Springmann *et al.*, 2018). Because the production of plant-based foods is invariably much more efficient when compared to animal counterparts (Nijdam *et al.*, 2012; Davis *et al.*, 2016; Gephart *et al.*, 2016; Clark & Tilman, 2017; Poor & Nemecek, 2018), diet preferences have consistently been found to be the most important determinant of agricultural land requirement (Alexander *et al.*, 2016; Donati *et al.*, 2016; Erb *et al.*, 2016a). It is thus urgent to identify opportunities in the consumption/demand side of human carnivory.

Fortunately, such opportunities certainly exist. First, humans are facultative carnivores, meaning there are no physiological constraints to the substitution of animal-based foods by plant-based alternatives (Craig *et al.*, 2009; Clarys *et al.*, 2014; Schüpbach *et al.*, 2015). Second, plant-based diets have in fact been consistently associated with lower prevalence of obesity, hypertension, diabetes, cardiovascular diseases, and several common types of cancer (e.g., Key *et al.*, 2014; Le & Sabaté, 2014; Yokoyama *et al.*, 2014; Dinu *et al.*, 2017). Third, reducing the consumption of animal products not only has the potential to solve public health issues associated with excessive consumption, but also those

related to insufficient nutrition, as competition between the production of livestock feed and human food seriously undermines food security (Cassidy *et al.*, 2013; Billen *et al.*, 2015; Davis & D'Odorico, 2015; Di Paola *et al.*, 2017). Such health and social benefits of curbing the demand for meat and dairy, added to the positive environmental outcomes of land and water sparing, and climate change and pollution mitigation, are increasingly leading to authoritative recommendations of a global shift towards more plant-based diets (e.g., Tilman & Clark, 2014; Westhoek *et al.*, 2014; Springmann *et al.*, 2016; Ripple *et al.*, 2017; Willett *et al.*, 2019).

Like virtually any desirable revolution, the implementation of the recommended dietary transition certainly faces sociocultural and political obstacles, which tend to weaken as more evidence of the necessity to transformation emerges. Along its three chapters, this thesis aims to improve our understanding and raise awareness on (1) the full impact of human carnivory on other species, (2) the area-related implications of livestock production to human well-being, and (3) the real nature conservation and human development opportunities generated by the adoption of more plant-based diets. Hopefully, the results and recommendations of this thesis might contribute to a make the trophic ecology of our species a central issue for environmental policy.

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CHAPTER 1

Human carnivory as the major driver of vertebrates' extinction

Abstract

Although a considerable amount of past and present anthropogenic impact on other species is known to be caused by our habit of eating other animals, little attention has been given to understanding and quantifying how this ecological aspect of our species threatens biodiversity globally. In this study, we reviewed the anthropogenic threats to 1,000 species randomly selected among more than 46,000 vertebrate entries in the International Union for the Conservation of Nature 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 predation-related mechanisms (predation and bycatch), two competition-related mechanisms (prey depletion and persecution), one mechanism associated with biohazards, four mechanisms associated with environmental changes (destructive harvesting practices, livestock, agriculture, and climate change), and a miscellaneous category for processes with more indirect connections with our high position in the food chain. Livestock and predation threaten a higher proportion of terrestrial and freshwater vertebrates, while marine species are primarily imperiled by predation and bycatch. Overall, aquatic species tend to be more affected by human carnivory than terrestrial species. We conservatively estimate that approximately one-quarter of the world's vertebrates is 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 infrastructure, logging, pollution, energy production and mining, and climate change. Moreover, we found that the number of mechanisms related to human carnivory affecting species is positively correlated with species' extinction risk. Our results suggest that human carnivory is the major driver of the current biodiversity crisis, and we hope the numbers we present here might contribute to raise awareness about this fundamental yet overlooked aspect of human ecology.

Keywords: biodiversity crisis, bycatch, human ecology, livestock, predation, trophic ecology.

Introduction

Woolly mammoths and rhinos, hippo-like marsupials, giant sloths and giant elks. These are just a few of the Pleistocene's megafauna species that have gone extinct as *Homo sapiens* spread from Africa and colonized other continents. It now seems well established that the human impacts have been the major cause of extinction of all these species (Sandom *et al.*, 2014; Bartlett *et al.*, 2016; Johnson *et al.*, 2016; Surovell *et al.*, 2016; Araujo *et al.*, 2017). Marsupial lions, cave bears, and saber-tooth-tigers are examples of animals that have gone extinct around the same period, presumably not because of direct hunting, but possibly because of prey scarcity and even direct competition with humans (Martin & 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 has justifiably implicated us as the driver 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 *et al.*, 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 & Shine, 2016). The construction of infrastructure for human settlements, transportation, and commercial and industrial activities, the agriculture and aquaculture sectors, the energy production and mining industries, and the harvest of biological resources are among the activities that affect ecosystems and biodiversity worldwide (Salafsky *et al.*, 2018). 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; Alexander *et al.*, 2015; Machovina *et al.*, 2015; Ripple *et al.*, 2015; Davis *et al.*, 2016; Frank *et al.*, 2016; Clark & 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; Foley *et al.*, 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 area (Steinfeld *et al.*, 2006; Cassidy *et al.*, 2013). Thus, the livestock sector is currently the single major driver of terrestrial natural habitats loss and degradation, which is in its turn a leading cause of species decline and extinction worldwide (Vié *et al.*, 2009; Ducatez & Shine, 2016).

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, 2018a). 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 & Tanaka, 2004; Camargo & Alonso, 2006; Diaz & 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 pre-historic 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 (Gariné-Wichatitsky *et al.*, 2013; Krkošek *et al.*, 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 so often escape into the wild (Laikre *et al.*, 2010). These same detrimental interactions have been reported for wild animals introduced in natural habitats where they did not previously occur in order to be latter harvested for human consumption (Ogutu-Ohwayo *et al.*, 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 (GHG) emissions (Gerber *et al.*, 2013), and for 74% of GHG derived from the global food production system (Davis *et al.*, 2016). Such emissions are behind global climate change, which affects the planet's biodiversity in various and unpredictable ways. Indeed, weather-related disruption of habitats has been an issue of major concern (Filipe *et al.*, 2013; Segan *et al.*, 2016), especially in highly endangered, biodiverse, and ecologically important systems such as coral reefs and sea prairies (Hoegh-Guldberg *et al.*, 2007; De'ath *et al.*, 2012; Chefaoui *et al.*, 2018). By making the environmental conditions unsuitable for species' persistence, climate change can force them to migrate to higher latitudes and altitudes, often with unpredictable consequences for the local biota (Lejeusne *et al.*, 2009; Raitos *et al.*, 2010). Furthermore, climate change is known to facilitate the global spread of diseases, such as the infection caused by the fungi *Batrachochytrium dendrobatidis* and *B. salamandrivorans*, a major cause of amphibian's sharp decline worldwide (Pounds *et al.*, 2006; Wake *et al.*, 2008). In addition to these mechanisms, many others such as bycatch (Lewinson *et al.*, 2014; Oliver *et al.*, 2015), direct competition (Curry *et al.*, 2011; Wolf & Ripple, 2016), retaliation against other

predators (Inskip & Zimmermann, 2009), and killing animals such as dolphins and caimans to produce bait (Mangel *et al.*, 2010; Brum *et al.*, 2015) classify as ways by which the high position of humans in the food chain affects biodiversity.

The multiple, synergetic, and ubiquitous past and present processes by which human carnivory threatens the world's biodiversity makes this ecological aspect of human populations arguably the single most detrimental to species conservation (Machovina *et al.*, 2015). However, to our knowledge, a systematic review of such processes has not been conducted, and their impact on taxonomic and ecological groups remain overlooked. In this study, we offer a comprehensive review of the direct and indirect mechanisms by which the high position of humans in the global food chain 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, systems and realms) 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.

Methods

The International Union for the Conservation of Nature (IUCN) Red List database presently includes 46,557 vertebrate species, distributed among the taxonomic classes Myxini (the group comprising the hagfish), Cephalaspidomorphi (lampreys), Chondrichthyes (cartilaginous fish), Actinopterygii (ray-finned fish), Sarcopterygii (lobe-finned fish), Amphibia (frogs, salamanders, and caecilians), Reptilia (reptiles), Aves (birds) and Mammalia (mammals). To each species, a

threat category is attributed. Threat categories reflect species' extinction risk: Least Concern, Near Threatened, Vulnerable, Endangered, Critically Endangered, Extinct in the Wild, and Extinct. A species is considered threatened with extinction when it is classified as Vulnerable, Endangered, or Critically Endangered. Species to which the available information is insufficient to assign a threat category are indicated as Data Deficient (IUCN, 2012). 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), systems (terrestrial, freshwater, marine), and realms (the largest biogeographical regions, such as Neotropical and Palearctic) where each species occurs. A single species can be present in more than one habitat, system or realm (Table S1).

In this study, we merged the five fish classes in a group including all fish species. Using a random data sampling without reposition in R environment, we selected 1,000 vertebrate species (Table S2). To assess whether the random sample could be considered representative of the whole IUCN dataset for vertebrates, we compared the number of species within each class in the sample with the proportion of species within each class in the entire dataset using a one sample Chi-square test. The same test was performed to systems, realms, and threat categories (Table S3). We then reviewed the fields “threats” and “threats

list” of those 1,000 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). To improve the detection of cases where human carnivory affects vertebrates through biohazards, we used the IUCN Global Database of Invasive Species (GDIS, 2019). We considered the 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 baits, contaminant nursery material, contaminant bait, and angling/fishing aquaculture equipment (Table S4).

Mechanisms were considered to impact species independently of being related to past, present, or future threats, and independently of threats' intensity. The information in the fields “threats” and “threats list” of the dataset was carefully read and compared for coherence before assigning each species with any mechanism. When these fields reported equivocal or conflicting information, the mechanism in question was not attributed. For example, although the passerine bird *Pyrrhula murina* is reported to be threatened by hunting and trapping of terrestrial animals in the field “threats list”, it was not attributed with the mechanism predation, as the field “threats” says nothing about the purpose of harvest. 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 if it was indicated to be of commercial interest for fisheries in the FishBase (FishBase, 2019). The agriculture and livestock mechanisms were not included in the quantitative analysis because the information in “threats” and “threats list” field alone does not allow disentangling the cases in which croplands and related impacts and climate change are driven by the production of livestock. As only two and four species within the sample occur in oceanic deep benthic habitat and in the Antarctic realm (respectively), these ecological groups were not included in the analysis neither.

We recorded the proportion of species affected by each mechanism, according to taxonomic and ecological categories. The taxonomic categories include fish (as defined above), amphibians, reptiles, birds, and mammals, while the ecological categories group species according to the habitats, systems, and realms they inhabit, as reported by the IUCN Red List. We also estimated the proportions of vertebrates as a whole, as well as vertebrate species within each taxonomic or ecological group that are affected by at least one of the identified mechanisms. In all cases, the proportion of species within each threat category was also presented.

As a matter of comparison, we also produced an estimate of the proportion of vertebrates that are affected by the following aspects of human ecology: agriculture, infrastructure, use of wild plants, pollution, invasive species, natural system modifications, energy production and mining, and climate change. To do so, we used (1) the Unified Classification of Direct Threats (version 3.2) adopted by the 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).

Finally, we used Pearson's correlation to investigate whether the number of mechanisms related to human carnivory affecting species (given by the column “Total” in Table S2) correlates with species' threat level. Threat level was generated by attributing values from 0 to 5 to threat categories from Least Concern to Extinct, respectively (the threat category Extinct in the Wild was not present in the 1,000 species sample) (Table S2).

Results

Among the 1,000 randomly selected species, we recognized two predation-related mechanisms (predation and bycatch), two competition-related mechanisms (prey depletion and persecution), one mechanism associated with biohazards, four mechanisms associated with 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 full description of these 10 mechanisms is presented in Table 1.

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 fish allowed to roam in the wild. Mechanisms marked with an * were not included in the quantitative analysis.

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		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.
	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.

When all vertebrates are considered, predation affects the highest proportion of species (11.9%), followed by livestock (10.8%), bycatch (5.4%), and biohazards (3.3%) (Figure 1A). For birds and mammals, predation and livestock are also the two most impacting mechanisms (Figures 1E and 1F). In the case of fish, the role of livestock as the second most impacting mechanism is replaced by bycatch (Figure 1B), while for amphibians and reptiles, livestock is by far the most prominent menace (Figure 1C and 1D). Biohazards have the highest impact in species that inhabit aquatic environments (Figures 1B and 1C). 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 fish and reptiles ($\approx 18\%$). Respectively, livestock threatens 27.2%, 18%, and 13.6% of amphibians, reptiles and mammals, while predation affects 23.2% and 18.5% of mammals and fish (Figure 1).

It is worth noting the high representativeness of species threatened with extinction (i.e., those classified as Vulnerable, Endangered, or Critically Endangered) within the proportion of affected species across many taxonomic and ecological groups (Figures 1, 2, 3 and 4).

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 respectively more than 40% and 20% of oceanic and neritic dwellers. 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 (Figure 2).



Figure 1. Proportion of vertebrate taxonomic groups affected by the mechanisms related to human carnivory, distributed by the IUCN Red List's threat categories. The bars are not additive, as a single species might 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 S5 for detailed values.

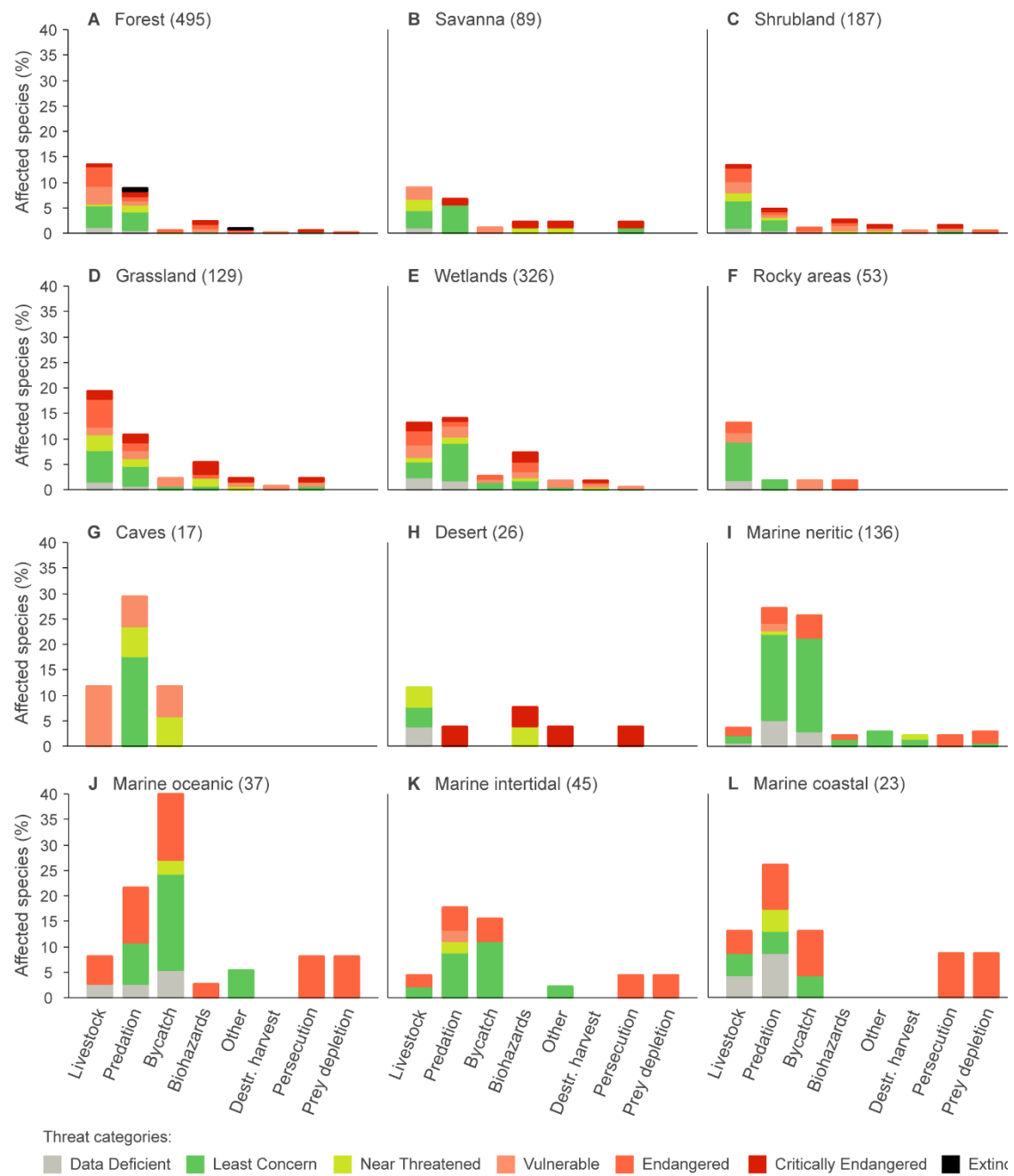


Figure 2. Proportion of vertebrate species grouped by habitat of occurrence that is affected by the mechanisms related to human carnivory, distributed by the IUCN Red List's threat categories. Some species occur in more than one habitat. All the rest is like in Figure 1. See Table S6 for detailed values.

A pattern similar to the previously described for classes and habitats 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 (Figure 3A and 3B). 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 (Figure 3C).

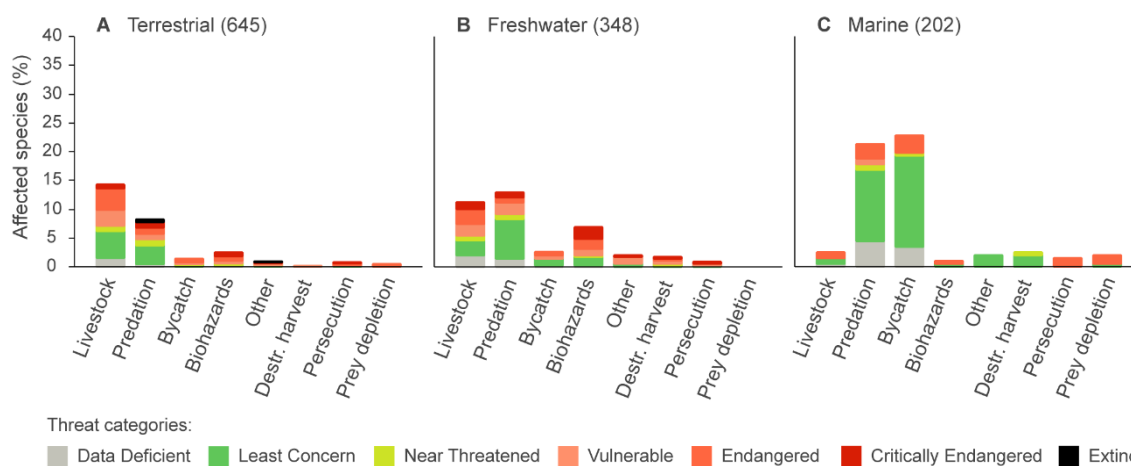


Figure 3. Proportion of vertebrate species grouped by system of occurrence that is affected by the mechanisms related to human carnivory, distributed by the IUCN Red List's threat categories. Some species occur in more than one system. All the rest is like in Figure 1. See Table S7 for detailed values.

When biogeographical realms are considered, livestock, predation and bycatch have a comparable impact on the world's vertebrates. Depending on the realm of occurrence, livestock, predation, and bycatch respectively threaten 4.3-16.2%, 7.2-20.3%, and 2.9-16.2% of all vertebrate species. To vertebrates inhabiting Australasian and Palearctic realms, the impacts from biohazards

related to human carnivory are also worth noting, as at least 6% of the species are affected by this mechanism (Figure 4).

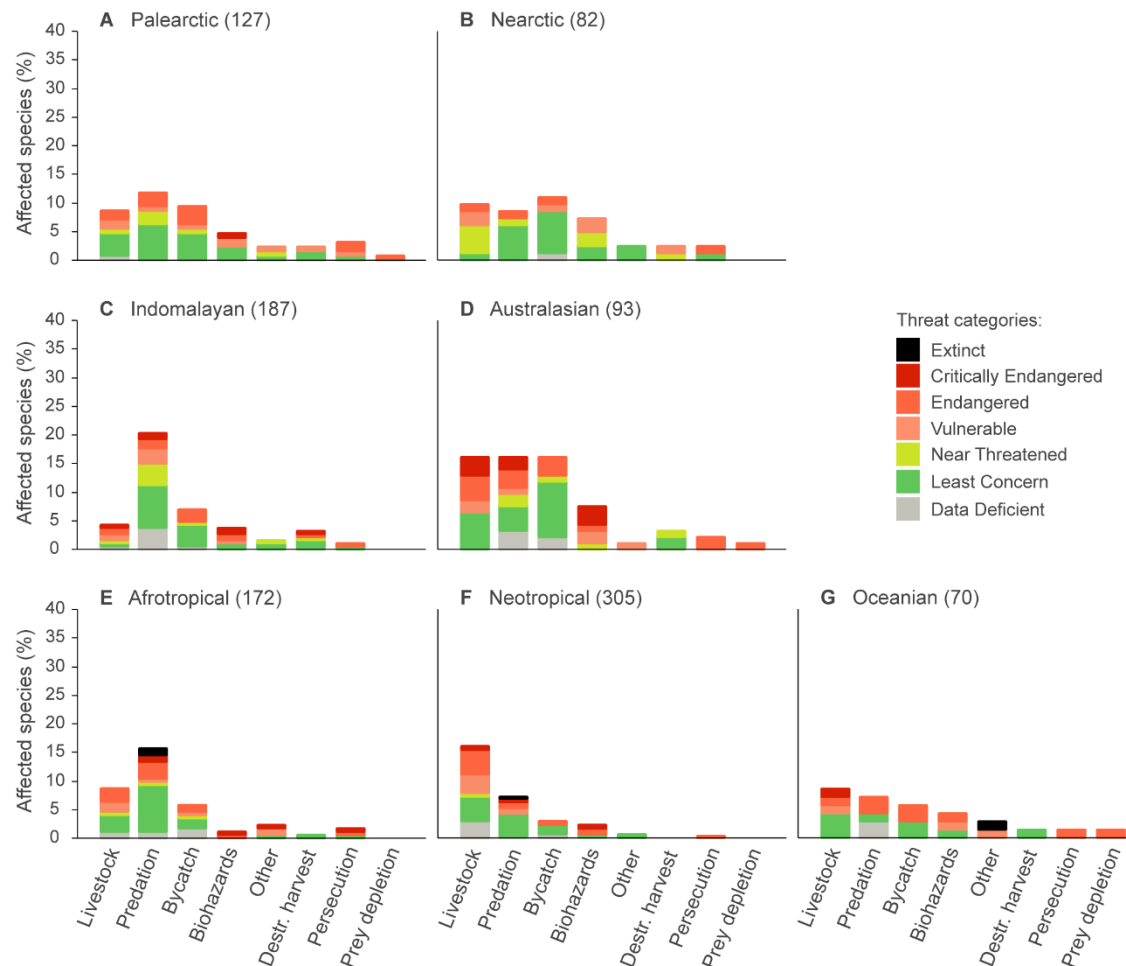


Figure 4. Proportion of vertebrate species grouped by realm of occurrence that is affected by the mechanisms related to human carnivory, distributed by the IUCN Red List's threat categories. Some species occur in more than one realm. All the rest is like in Figure 1. See Table S8 for detailed values.

Human carnivory threatens 26.1% of the 1,000 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 fish, mammals, amphibians, species that occur in oceanic, neritic, and coastal marine habitats, as well as in caves and subterranean habitats and inland wetlands, marine systems, and the Australasian realm, of which 30% or more species are affected. Overall, aquatic species tend to be more affected by human carnivory than terrestrial species (Figure 5).

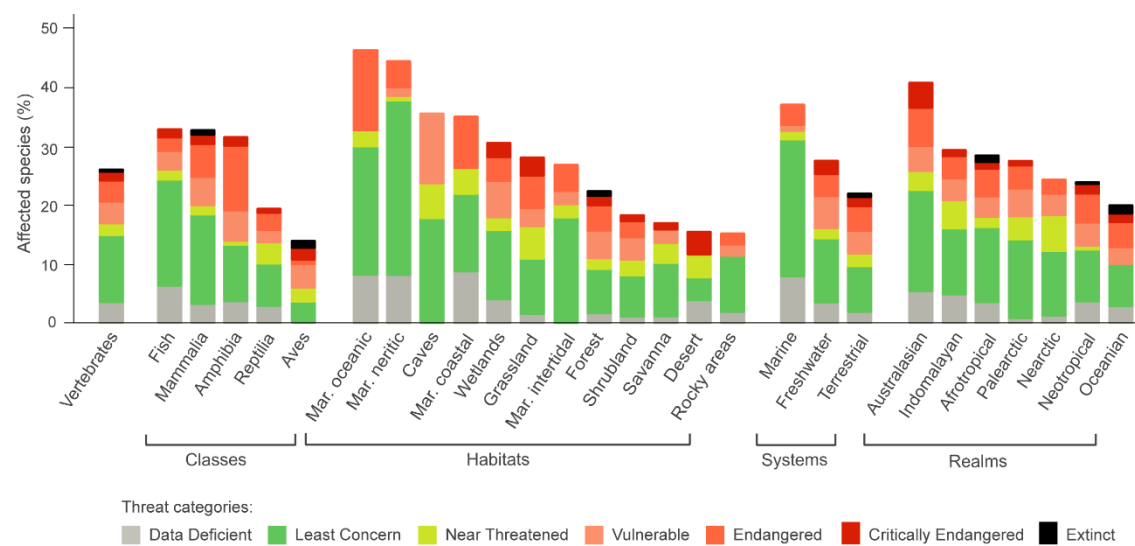


Figure 5. Proportion of vertebrate species within taxonomic and ecological groups, and distributed by the IUCN Red List's threat categories, that is threatened by at least one of the following mechanisms related to human carnivory: predation, bycatch, prey depletion, persecution, biohazards, destructive harvesting practices, livestock, and other. These values are based on 1,000 entries randomly selected from the 46,557 vertebrate species in the IUCN database. See Table S9 for detailed values.

Carnivory is the second most impacting aspect of human ecology in terms of the proportion of species (26.1%), species threatened with extinction (45.1%), and species with decreasing populations (39.5%) it affects. Among the eight remaining assessed ecological aspects, only agriculture, which includes the production of livestock, had a higher impact (Table 2). Finally, we found that species' threat level is positively correlated with the number of mechanisms related to human carnivory affecting them ($T = 8.178$, $P < 0.001$).

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 1,000 entries randomly selected from the 46,557 vertebrate species in the IUCN Red List database. Proportions were calculated considering the 1,000 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. Ecological aspects are ranked by decreasing number of species they affect. Note that about 70% of agricultural area and related impacts are attributable to livestock production (Steinfeld *et al.*, 2006), which explains the higher number of species affected by agriculture when compared to carnivory.

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)
Agriculture	Terrestrial farming and ranching and associated pollution and water use.	Annual and perennial non-timber crops (2.1), wood and pulp plantations (2.2), livestock farming and ranching (2.3), abstraction of surface water (agricultural use) (7.2.3), abstraction of ground water (agricultural use) (7.2.7), agricultural and forestry effluents (9.3).	283	28.3%	134	68.7%	146	57.7%
Carnivory	Human habit of feeding on other animals.	Predation, bycatch, prey depletion, persecution, biohazards, destructive harvesting practices, livestock, and other.	261	26.1%	88	45.1%	100	39.5%
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%
Wild plants use	Consumptive use of wild biological resources from plant species.	Gathering of terrestrial plants (5.2), logging and wood harvesting (5.3).	165	16.5%	82	42.1%	92	36.4%
Pollution	Introduction of exotic and/or excess materials or energy.	Pollution (9).	111	11.1%	53	27.2%	51	20.2%

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)
Invasive and other problematic species, genes and diseases	Non-native and native plants, animals, pathogens/microbes, or genetic materials that have or are predicted to have harmful effects on biodiversity following their introduction, spread and/or increase in abundance.	Invasive and other problematic species, genes and diseases (8).	104	10.4%	67	34.4%	57	22.5%
Natural system modifications	Habitats conversion or degradation after managing of natural or semi-natural systems to improve human welfare.	Natural system modifications (7).	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 of the natural range of variation.	Climate change (11).	71	7.1%	33	16.9%	33	13.0%

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 that are impacted by these mechanisms. Our findings also 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. This suggests our habit of feeding on other animals might explain much of the global continuing decline of the world's vertebrates despite the ongoing conservation efforts (Hoffmann *et al.*, 2010; Tittensor *et al.*, 2014). Although our results are based on a sample of the total list, as the observed number of species within each group and threat category in the sample does not significantly differ from the expected values (Table S3), our results can be considered representative of and applicable to all vertebrates.

Agriculture and climate change were identified as mechanisms by which human animalivory impacts vertebrates, because about one-third of the world's crops are allocated as livestock feed (Steinfeld *et al.*, 2006), and the livestock sector accounts for 15% of all GHG emissions (Gerber *et al.*, 2013). However, as the IUCN Red List's dataset does not allow disentangling livestock's share in total agriculture and total climate change from that of other contributors, the proportion of vertebrates affected by these two mechanisms was not included in the quantitative analysis. As agricultural activities and climate change affect biodiversity in such a permeating way, we argue our results are a very 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 (Figure 5; Table 2).

Nonetheless, we found carnivory to be the second aspect of human ecology in terms of the proportion of species, of species threatened with extinction, and of species with decreasing populations it affects. Of the other assessed ecological aspects, including all kinds of infrastructure and pollution, logging, energy production and mining, and climate change, only agriculture had a higher impact (Table 2). However, because 70% of global agricultural area and related impacts are actually driven by the production of livestock (Steinfeld *et al.*, 2006), we argue carnivory is indeed the number one aspect of human ecology driving the global biodiversity crisis. If we are to solve the current decline and extinction rates afflicting the world's vertebrates, it is crucial to acknowledge the ultimate drivers behind them and properly measure their impact. This includes recognizing that the impacts of animal-based foods are ecologically and quantitatively different from the impacts caused by the production of vegetal equivalents, supporting the idea that treating them both as general agriculture hinders the identification of practical solutions to this highly destructive facet of our species (Graesser *et al.*, 2015). To our knowledge, this is the first study aiming to quantify the impacts of human carnivory and compare them with those attributable to other ecological aspects of our populations.

Overall, we found livestock and predation to be the mechanisms most affecting vertebrates that inhabit terrestrial and freshwater habitats and systems, while marine species are primarily threatened by predation and bycatch. Habitat alteration, which comprises all forms of degradation related to land-use change, water cycle change, and pollution, is the main cause of species decline and

extinction worldwide (Ducatez & Shine, 2016), and grazing and mowing are the more widely spread land-management activities (Erb *et al.*, 2016). This 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 & 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 terrestrial plants”, further contributing to underestimate the real impacts of livestock. Moreover, marine species inhabiting coastal and coral reef habitats, which comprise the majority of fish diversity, are known to be severely affected by pollution associated with land-use change (Islam & Tanaka, 2004; Diaz & 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; Ripple *et al.*, 2019). Thus, the high proportion of species affected by predation across realms 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. Having this in mind, it is interesting to note the realms we found to be more affected by predation correspond to previous assessments on where most bushmeat hunting occurs (Ripple *et al.*, 2016).

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 (Figure 5). As fish represent approximately 35% of all vertebrate species (Table S3), and as impacting fisheries occur all over the globe, high levels of bycatch are observed across all realms. As bycatch threatens a higher proportion of marine species than predation itself (Figure 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 is 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 diseases 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, as in the case of the cyprinid *Gambusia clarkhubbsi*. 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 fish, amphibians, and species inhabiting inland wetlands and grasslands. Freshwater fish and amphibians, as the Critically Endangered cyprinid *Barbodes palata* and the salamander *Ambystoma amblycephalum*, commonly suffer from deleterious interactions with introduced fish released in the wild to be later harvested for human consumption. Additionally, amphibians, which are less agile animals and often have fossorial habits, are also prone to trampling by free ranging and feral ungulates (e.g., the frog *Litoria rheocola*). Concerning species inhabiting grasslands, the relatively high impact of biohazards mechanism is due to competition with free ranging and feral livestock, as these habitats are widely used as pastures (Suttie *et al.*, 2005).

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 & 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 & Zimmermann, 2009; Ripple *et al.*, 2014). As the loss of top

predators completely alters entire ecosystems in complex and unpredictable ways (Strong & 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 & Folke, 1999; Orth *et al.*, 2006).

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, the subtlety and complexity of these 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 including all the available information on species interactions in conservation assessments such as the IUCN Red List.

Conclusion

Our very conservative estimate reveals that human carnivory is the single ecological aspect of our species that most threatens the world's vertebrates, mainly through the mechanisms of livestock production, predation, and bycatch. We highlight that competition-related mechanisms, as well as detrimental interactions with invasive species ultimately associated with our habit of eating other animals, are also main threats within certain groups, such as carnivores and freshwater species, respectively. These findings, which support the piling evidence that the high position of humans in the food chain plays a critical role in the ongoing biodiversity crisis (e.g., Cassidy *et al.*, 2013; Machovina *et al.*, 2015; Alexander *et al.*, 2016; Davis *et al.*, 2016), indicate that curbing the consumption of animal-based foods would have a beneficial effect on the world's vertebrates. As human carnivory conservatively affects one-quarter of all vertebrates in many and synergetic ways, a dietary shift towards more plant-based diets might be indeed one of the most promising strategies to reduce our global impact on biodiversity, and should thus be a leading focus for environmental policy. We believe that the numbers we present here are a much needed and powerful tool to raise awareness about the impacts of human carnivory on the world's biodiversity, and that including the proportion of agriculture and climate change attributable to the production of livestock would further contribute to call for urgent intervention. If we are to halt the biodiversity crisis that started 10,000 to 50,000 years ago and has lingered on to the present time, efficient strategies to reduce human consumption of animal products need to be globally implemented, as this major yet overlooked aspect of human ecology has been a leading cause of species decline and extinction ever since.

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Supplementary Material

Available at:

<https://drive.google.com/open?id=1ps8BrVhK3ecNRNgHwqAhGrNmoPgMhi83>

Table S1. The 46,557 vertebrate species and respective data obtained from the IUCN Red List database.

Table S2. The 1,000 vertebrate species and respective data randomly selected from the 46,557 entries in the IUCN Red List database. These 1000 species were used to (1) identify the mechanisms by which human carnivory threatens the world's vertebrates, (2) quantify the proportion of species affected by each one of these mechanisms, and (3) quantify the proportion of species affected by each aspect of human ecology (including carnivory). Values 1 and 0 were used to indicate whether each assessed species is affected by a given mechanism or ecological aspect or not, respectively. Threat level was generated by attributing values from 0 to 5 to threat categories from Least Concern to Extinct, respectively. The total number of mechanisms affecting each species is also indicated. See Tables 1 and 2 for full description of mechanisms and other aspects of human ecology, respectively.

Table S3. Number of species that belong to each group of vertebrates in the IUCN Red List dataset and in the random sample of 1,000 species obtained from the former, as well as the proportion of each group in relation to the total species quantity in respective dataset. As a given species might inhabit more than one habitat, system, or realm, the proportions of these groups were calculated by dividing their absolute number of species by the sum of the absolute number of species in all habitat, system or realm groups. The results of the chi-square tests performed to assess whether the sample is representative of the IUCN dataset are also given.

Table S4. Invasive species that were introduced via pathways related to human carnivory obtained from the Global Database of Invasive Species. Species

introduced to be hunted solely for their fur (*Castor canadensis* and *Vulpes vulpes*) and domestic dogs (*Canis lupus*) were not considered (indicated with NA). Taxonomic (kingdom, phylum, class, order, and family) and ecological (system and impact on native species) information is also given.

Table S5. Proportion of vertebrate taxonomic groups affected by the mechanisms related to human carnivory, distributed by the IUCN Red List's threat categories. 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.

Table S6. Proportion of vertebrate species grouped by habitat of occurrence that is affected by the mechanisms related to human carnivory, distributed by the IUCN Red List's threat categories. Some species occur in more than one habitat. As only two species occur in oceanic deep benthic habitat, this habitat was not included in the analysis. 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 assessed species that occur in each habitat.

Table S7. Proportion of vertebrate species grouped by system of occurrence that is affected by the mechanisms related to human carnivory, distributed by the IUCN Red List's threat categories. Some species occur in more than one system. 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 assessed species that occur in each habitat.

Table S8. Proportion of vertebrate species grouped by realm of occurrence that is affected by the mechanisms related to human carnivory, distributed by the IUCN Red List's threat categories. Some species occur in more than one realm. As only four species occur in the Antarctic realm, this realm was not included in the analysis. 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 assessed species that occur in each realm.

Table S9. Proportion of vertebrate species within taxonomic and ecological groups, and distributed by the threat categories adopted by the IUCN Red List, that is 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 1,000 entries randomly selected from the 46,557 vertebrate species in the IUCN database.

CHAPTER 2

The wilder the happier:

Natural land cover correlates with human well-being at country level

Abstract

The conversion of natural habitats into agricultural land, mostly driven by the production of livestock, is rapidly depleting the natural resources and diminishing the ecosystem services human populations depend on. Besides, it is also the main cause of biodiversity decline in terrestrial ecosystems. At the same time, emergent research has shown nature experience plays a critical role in the well-being of humans at local level. Although long-term human development and nature conservation are interdependent goals, the relation between natural environments and human well-being at large scales is essentially unknown. The United Nations' Human Development Index (HDI) accounts for the health, education, and income dimensions of each country, and these socio-economic variables are highly correlated with overall life satisfaction. Here we show the percentage of natural land cover is also positively correlated with human well-being, as adding this variable to the socio-economic model better predicts the global variation of life satisfaction. We also discuss the environmental and social consequences of livestock production with special emphasis on countries with low and middle HDI levels, where most deforestation and food insecurity occur. We recommend the inclusion of the natural land cover index in the HDI as the environmental dimension it currently lacks. The Environmentally-adjusted Human Development Index here proposed could be a powerful inducer of public policy

by encouraging actions towards both nature conservation and human well-being aspirations in an planet increasingly dominated by artificial landscapes.

Keywords: ecosystem services, food security, life satisfaction, Human Development Index, land-use change, livestock.

Introduction

As all other animal species, humans rely on nature. Our existence and wealth depends on a variety of services freely delivered by ecosystems, such as water and food supply, raw materials, and climate regulation, whose value can be estimated according to the different land cover types and their area (Costanza *et al.*, 1997; de Groot *et al.*, 2012). As the growing human populations with rising consumption levels pose increasing pressure on natural environments, the provision of such services becomes seriously at risk (Sanderson *et al.*, 2002; Foley *et al.*, 2005; de Groot *et al.*, 2012; Watson *et al.*, 2016). Not only the value of natural ecosystems per unit of area is higher when compared to artificial landscapes (i.e., croplands and urbanized areas) (Costanza *et al.*, 1997), but the intensive use of artificial environments often implies further reduction of their ability to generate environmental services (Sutton *et al.*, 2016). Of the 130 Mkm² of ice-free land on the planet, approximately 80% is managed under schemes of varying intensity. Grazing and mowing is the more widely spread land management activity, occupying 46.9 Mkm² ($\approx 36\%$) of ice-free land, followed by forestry (29.4 Mkm², $\approx 23\%$) and cropland (15.2 Mkm², $\approx 12\%$) (Erb *et al.*, 2016b). Moreover, about one-third of global cropland's production is used as stall feed (Steinfeld *et al.*, 2006; Cassidy *et al.*, 2013), making the livestock sector

overwhelmingly the single major driver of land-use change and related environmental problems worldwide. In its turn, the ongoing rate of land-use change and associated impacts not only undermines the future of human populations, but is also a leading proximate cause of the global biodiversity decline (Vié *et al.*, 2009; Ducatez & Shine, 2016). This suggests a compatibility between human well-being and nature conservation at large scales and in the long-term.

In addition to the tangible benefits previously described, the experience of nature provides a range of psychological well-being, cognitive, physiological, social, and spiritual benefits to humans (Keniger *et al.*, 2013). Approximately 56% of all human beings spend their daily lives in urban environments (United Nations, 2018). As the growing human populations aggregate in sprawling cities, more people are deprived from the close contact with the natural environments that have shaped our bodies, our brains, and our behavior through the evolution of our species (Antón *et al.*, 2014). This deprivation is known to have negative consequences for human well-being, and physical and mental health conditions ubiquitously threaten urban dwellers' life quality (Sundquist *et al.*, 2004; Goryakin *et al.*, 2013). Indeed, it has been shown that urban greenspaces are critical to the improvement of city inhabitants' health and well-being (Shanahan *et al.*, 2016; Engemann *et al.*, 2019). Moreover, the psychological benefits of an urban greenspace increase with species richness (Fuller *et al.*, 2007), and individuals' environmentally friendly behavior increases after experiencing contact with nature (Hartig *et al.*, 2007; Soga & Gaston, 2016). The high demand for natural places – the world's protected areas receive roughly 8 billion visits per year (Balmford *et al.*, 2015) – shows how important they are for human well-being,

reinforcing the idea of interdependence between environmental and human aspirational goals.

The United Nations' Human Development Index (HDI) is the most widely used composite index to assess countries' development. It focus on the health, education and income dimensions of human societies, which are expressed by four socio-economic components: life expectancy at birth (LEB), expected years of schooling (EYS), mean years of schooling (MYS), and gross national income per capita (GNI) (United Nations, 2016). Despite the recognized importance of nature to human well-being, the development concept behind the HDI fails to account for the environmental dimension of human societies. Subjective perceptions of well-being accompany the HDI as supplementary indicators. Among these, the overall life satisfaction index (OLSI) accounts for how, on average, the individuals of a country feel about their own lives (United Nations, 2016). This self-reported well-being measure is known to be correlated with the dimensions included in the HDI (Oishi & Diener, 2014).

Understanding the benefits of people-nature interactions has great potential to improve both human well-being and nature conservation. However, to our knowledge, no study as assessed the relationship between natural areas and human well-being at country level. Herein, we evaluate how countries' percentage of natural land cover (NLC) and protected land cover (PLC) relate with the overall life satisfaction of their inhabitants, after controlling for the socio-economic variables considered in the HDI. We also propose the Environmentally-adjusted Human Development and compare it with the standard HDI.

Methods

We performed a model selection to compare whether the models considering NLC and PLC were better in predicting the OLSI than the solely socio-economic model. Null models were used to assess the probability of our best model being selected by chance alone. By assessing the coefficients' size and their respective *P*-values, we also evaluated the relation between each variable of the selected model and the OLSI, while considering all countries, as well as countries within each HDI level as determined by the United Nations (United Nations, 2016). Using Pearson's *r* coefficients and their *P*-values, and considering all countries, we also assessed the correlation between the health, education, income, and NLC indices. Finally, we produced the Environmentally-adjusted Human Development Index (EHDI – which is given by the geometric mean of the health, education, income, and natural land cover indices) for the world's countries in the year 2015, and compare it with the standard HDI for the same year.

Assessing countries' socio-economic dimensions

We obtained the OLSI and the four components of the HDI for 2015 from the Human Development Report 2016 (United Nations, 2016). We followed the technical notes that accompany this document to produce the socio-economic variables considered in the candidate models. We calculated the health, education, and income indices by applying the formula

$$\text{Dimension index} = \frac{(\text{actual value} - \text{minimum value})}{(\text{maximum value} - \text{minimum value})}$$

to the four components of the HDI. The minimum and maximum values are respectively the natural zeros and aspirational goals. These values are 20 and 85 for LEB, 0 and 18 for EYS, 0 and 15 for MYS, and 100 and 75,000 for GNI.

Actual EYS and GNI values are capped at 18 and 75,000, respectively. The GNI index is calculated using the natural logarithm of the actual, minimum, and maximum values. The health and income dimension indices correspond to those of LEB and GNI, respectively, while the education dimension index is given by the arithmetic mean of EYS and MYS indices.

Assessing countries' NLC and PLC

To assess the percentage of NLC in each country we used a 2015 world land cover map with 300m resolution (ESA, 2016) and a 2015 world political map (ESRI, 2016a). Using ArcMap 10.4 (ESRI, 2016b), we projected these maps into a cylindrical equal area coordinate system (Behrmann World), adopting the spatial resolution of the original land cover map. During this process, the political map was also converted from vector to raster. The Spatial Analyst Tools' "combine" was used to assess the number of pixels by land cover category in each country. The original 22 land cover categories of the land cover map were pooled into two larger categories: artificial land cover (that included the five categories representing urban areas and cropland of all kinds, including mosaic of cropland with natural vegetation), and natural land cover (that included the remaining 17 categories). Knowing the total number of pixels per country (given by the sum of all the 22 land cover categories) and the total number of pixels corresponding to NLC, we calculated the percentage of each country's territory occupied by NLC, which was then divided by 100 to produce the NLC index. Similarly, we calculated the PLC index based on protected land area and total land area statistics for each country (WDPA, 2016). However, because no country has more than 50% of its territory under protected areas, the PLC percentage

was divided by 50 (instead of 100) to produce the PLC index. The NLC and PLC indices were calculated for the 187 countries for which the HDI dimensions were available (Table S1).

Model selection

We started by assessing the best way to use the health, education and income indices to predict the OLSI, by comparing two generalized linear models (GLMs). In the first, the OLSI was a function of the geometric mean of these three indices (i.e., a function of the HDI as commonly calculated; $OLSI \sim HDI$). In the second, the OLSI depended on the health, education, and income indices as separate variables ($OLSI \sim H + E + I$). The second model was selected as it provided a lower AIC_c value (Table 1), and was then used as the control model.

Based on the control model, we then built the alternative models, in which the OLSI depended on the health, education, income, and NLC or PLC indices ($OLSI \sim H + E + I + NLC$, and $OLSI \sim H + E + I + PLC$). This global analysis included the 156 countries for which the OLSI and the HDI dimensions were obtained (Table S1). Because the dependent variable followed a probability distribution of the Gamma family, we used this distribution and the inverse link function to run the GLMs. To identify the best supported models we considered low Akaike Information Criterion adjusted for small sample sizes (AIC_c), low delta values ($\Delta_i < 2$), and high values of Akaike weights (w_i) (Burnham & Anderson, 1998). To test whether the NLC index improved the selected model's performance by chance alone, we simulated a null AIC_c distribution by bootstrapping 10,000 times the NLC index, while maintaining the other three variables unchanged, for the 156 countries. We then tested if the AIC_c of the

selected model was significantly lower than the null distribution ($\alpha = 0.05$). All the analyses were performed in R 3.4.0 (R Core Team, 2016).

Results

The model considering the natural land cover index, besides the socio-economic variables, was the best supported among all candidate models (Table 1). Of the 10,000 null models only 240 (2.4%) had equal or better AIC_c values than the best model.

Table 1. Model selection criteria for the generalized linear models built to investigate the correlation between the overall life satisfaction index (OLSI) and the natural land cover (NLC) and protected land cover (PLC) indices. The health (H), education (E), and income (I) indices are considered in all models, and their geometric mean gives the Human Development Index (HDI). Sample-size adjusted Akaike Information Criterion (AIC_c), Akaike differences (Δ_i), Akaike weights (w_i), and number of parameters (K) are presented.

Model	AIC_c	Δ_i	w_i	K
OLSI ~ H + E + I + NLC	301.71	0	0.86	6
OLSI ~ H + E + I	306.12	4.41	0.09	5
OLSI ~ H + E + I + PLC	307.76	6.05	0.04	6
OLSI ~ HDI	311.85	10.14	0.01	3

In the selected model, the NLC index was found to be positively correlated with the OLSI ($P = 0.012$). The same was true for the health and income indices ($P = 0.009$ and $P < 0.001$, respectively), but not for the education index ($P > 0.1$). The NLC index was also positively correlated with the OLSI in countries with very

high and high HDI levels ($P = 0.030$ and $P = 0.013$, respectively), but not in countries with middle and low HDI levels ($P > 0.6$) (Figure 1; Table S2).

Regarding the data for the world's countries, the health, education and income indices are highly correlated with each other, while the NLC index is not correlated with any of these three socio-economic indices (Figure S1).

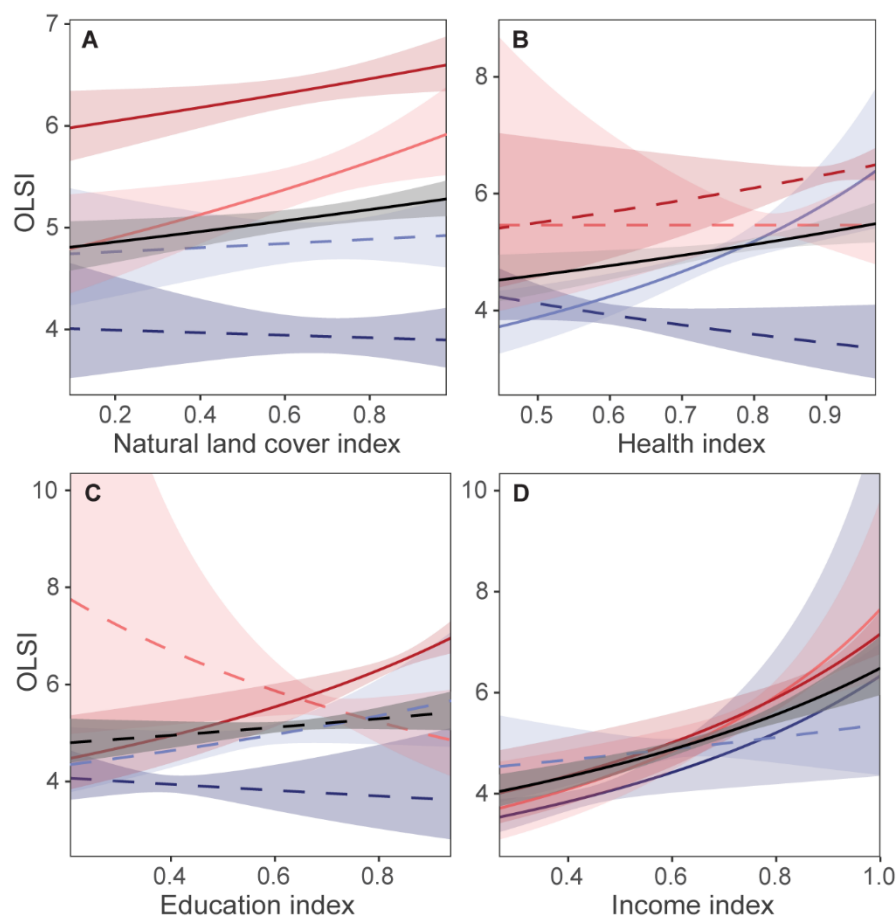


Figure 1. The effects of natural land cover (A), health (B), education (C), and income (D) indices on the overall life satisfaction index (OLSI) for all, very high, high, middle and low HDI levels (black, dark red, light red, light blue, and dark blue lines, respectively). Solid and dashed lines indicate significant and non-significant relations, respectively ($\alpha = 0.05$). See Table S2 for P -values.

Overall, there was a noticeable tendency for the Environmentally-adjusted Human Development Index values to be higher than the standard HDI for developing countries, while the opposite was verified for wealthier nations (Figure 2).

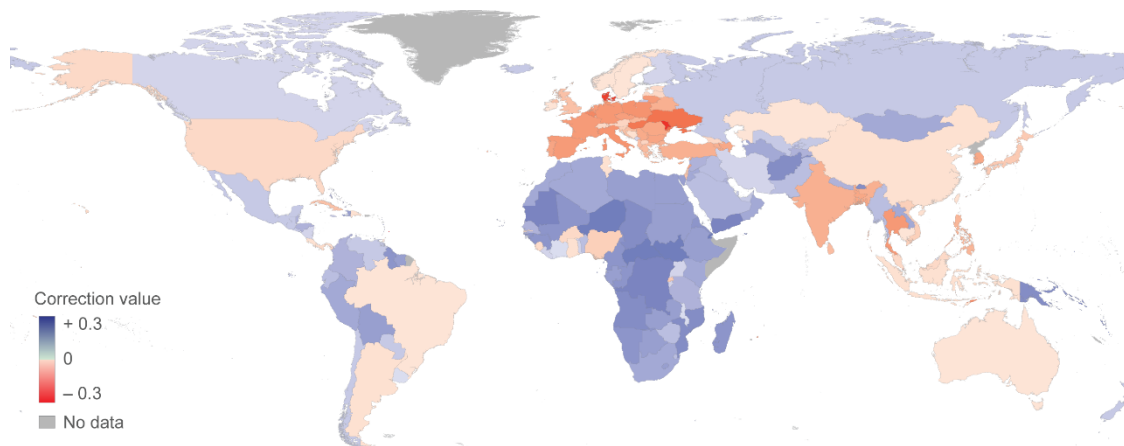


Figure 2. World map showing the difference between the Environmentally-adjusted Human Development Index and the Human Development Index for the year 2015. See Table S1 for detailed values.

Discussion

Our results show that adding the natural land cover (NLC) index to the Human Development Index (HDI) significantly improves its ability to predict the overall life satisfaction index (OLSI), revealing the existence of a significant positive correlation between nature conservation and the well-being of human populations at country level. While the OLSI is a known variable, identifying the factors affecting it is critical to define public policies aiming to improve human condition. As the HDI aims to reflect human well-being by considering dimensions other than income, we consider much appropriate to include the NLC index in this widely used development measure as the environmental variable it currently

lacks. We also believe further investigation of how to include the use of marine resources in this environmental dimension is an effort worth taking.

The case for considering the NLC index as a meaningful indicator of human well-being is strengthened by the finding that despite the NLC index is not correlated with any other of the three socioeconomic dimensions, it is correlated with the OLSI in a significant positive way, similarly to the health and income indices. Like the valuation of ecosystem services, the NLC index is also area-dependent, and has the advantage of offering a steady and easily available alternative way to estimate the benefits provided by nature to human populations. While the traditional valuation of nature considerably varies as more ecosystem services are associated with each biome (de Groot *et al.*, 2012), general natural land cover performs independently of the value per unit of natural land cover type. Moreover, emerging projects that periodically map the global terrestrial surface, such as the Climate Change Initiative of the European Space Agency, have led institutions like the Food and Agriculture Organization of the United Nations to freely publish tabular data on natural land cover by country for consecutive years (FAO, 2018).

Interestingly, the difference between the EHDI and the original HDI reveals a tendency of the later to overestimate the development of the countries with very high and high HDI levels, and to underestimate the development of the countries with low and middle HDI levels (Figure 2). This confirms the idea that generating socio-economic benefits often implies losing environmental benefits, thus reinforcing the importance of considering an environmental dimension when assessing human development. However, this conflict between the pursuit of socio-economic and environmental aspirations is not inevitable, as demonstrated

by countries like Canada, Finland, Iceland, and New Zealand (Figure 2). These are all countries with very low human population density (United Nations, 2017), implying this factor may be a condition for allowing the coexistence of these goals. On the other hand, it is important to acknowledge that, as rich countries are net importers of goods generated in foreign territories, they tend to externalize to poorer countries the environmental degradation associated with their high affluence (Lenzen *et al.*, 2012; Weinzettel *et al.*, 2013). This might also help explaining the environmental and socioeconomic success of the countries listed above. Especial attention should be given to countries like Bangladesh, Burkina Faso, Ghana, India, Indonesia, Nigeria, Philippines, Rwanda, Sierra Leone, and Vietnam, for which considering NLC lowers the HDI values, although these countries already have low and middle HDI levels. Notably, these countries have high population densities (United Nations, 2017), which reinforces the importance of demography to human well-being and nature conservation.

An inverse relation could be expected between NLC and life satisfaction in countries with low and middle HDI levels, as converting natural land cover into agricultural land should increase food security and income, and consequently well-being. However, such relation was not found in this study. This might be essentially explained by demographic and market factors, both exacerbated by a general change in consumption patterns. The nature of natural habitat loss and degradation in tropical regions, where most low and middle HDI countries are located, has changed in the last decades. Once caused by small-scale farmers and rural inhabitants, it is now primarily explained by high urban growth rates and increasing demand for agricultural products in distant urban and international locations (Butler & Laurence, 2008; DeFries *et al.*, 2010). While growing

population per se creates a higher need for food, urbanization in particular exacerbates this demand, as it is associated with higher incomes and consequently increased consumption of food products with heavier environmental footprints, such as meat, dairy, eggs, and vegetable oils (Kearney, 2010; Tilman *et al.*, 2011; Tilman & Clark, 2014; Alexander *et al.*, 2015). In Latin America, the conversion of natural ecosystems in the last decades has mostly been driven by the expansion of pasturelands and feed crops (Graesser *et al.*, 2015), which produce food for human populations through an indirect and much less efficient way than plants (Nijdam *et al.*, 2012; Alexander *et al.*, 2017; Clark & Tilman, 2017; Di Paola *et al.*, 2017; Poor & Nemecek, 2018). Additionally, only a fraction of agricultural yields is locally delivered, as much of the food and feed crops produced in Southeast Asia and Latin American agriculture is actually exported to wealthier countries (Naylor *et al.*, 2005; Weinzettel *et al.*, 2013). A similar situation is established in Southeast Asia, where not only livestock production but also palm oil plantations are behind high rates of deforestation associated with the food system (Rudel *et al.*, 2009; Koh *et al.*, 2011). Within the low HDI level countries – mostly Sub-Saharan African ones – a high fraction of cropland is dedicated to produce food crops (Foley *et al.*, 2011; Cassidy *et al.*, 2013). However, high population growth rates might check the increase in food production, resulting in a lack of significant negative relation between the NLC index and the OLSI.

Several solutions, such as closing ‘yield gaps’ on underperforming lands, increasing cropping efficiency, shifting diets, and reducing waste have been proposed to cope with the increasing demand for food without causing further environmental degradation (Foley *et al.*, 2011; Cassidy *et al.*, 2013). As diet

preferences are the most important determinant of agricultural land requirement, solutions from the consumption/demand-side have been considered necessary to ensure food security and environmental preservation in the coming decades (Alexander *et al.*, 2016; Donati *et al.*, 2016; Erb *et al.*, 2016a; Poore & Nemecek, 2018). While animal-based foods account for 87% of the agricultural land needed to feed a person with the current average diet, these products represent only 18% and 39% of caloric and protein intake, respectively (Davis *et al.*, 2016). Moreover, while rich countries are by far the primary consumers of meat and dairy, most deforestation caused by pastures and feed crops currently occurs in poorer tropical countries. Thus, the environmental costs of livestock production are mostly felt by more vulnerable and more fast growing populations, whose development aspirations and future needs greatly depend on healthy ecosystems.

Concomitantly with the dietary shift, promoting the reduction of fertility rates in low HDI level countries also constitutes an opportunity to curb the demand for additional agricultural area, as such countries are where much population growth is expected to occur in the coming decades (Montgomery, 2008). Low infant and child mortality rates constitute an important condition to spontaneously reduce fertility rates (Sachs, 2008; Mace, 2013). As deficient nutrition is still an important cause of mortality among the youngsters in poor nations (Pelletier *et al.*, 1995; Caulfield *et al.*, 2004), increased food security made possible by a more efficient use of agricultural area might also help reducing population growth.

Although the PLC index did not improve the socio-economic model in predicting the OLSI, this is possibly because most countries' percentage of PLC

is too low to have significant effects, and it does not mean the strategy of protecting natural areas in conservation units is not important for pursuing environmental and well-being goals. As strict protected areas characteristically prohibit land-use change, the widening of networks of such reserves can be crucial to guarantee high environmental dimension levels remain achievable in the future. However, it is important to have in mind that, in the real world, the creation of new protected areas and the continuity of those already existing have poor chances against heavy pressure to expand agricultural area, highlighting the importance of reducing the demand for less efficient foods.

Conclusion

Our large scale approach provides support for the idea that nature conservation and proper human development (i.e., the long-term well-being of human populations) are compatible and interdependent goals. The socio-economic variables being identical, the wildest countries are those that report higher levels of well-being, which is in accordance with the idea that natural environments provide precious benefits to our societies (Costanza *et al.* 1997; de Groot *et al.* 2012). The enormous role of the livestock sector in the conversion and degradation of natural habitats before its modest contribution to the global food production constitutes per se a reason to sustain that animal-based foods are a very inefficient way of feeding humanity, needlessly compromising the provision of vital ecosystem services we depend on. Besides, the asymmetry between the locales of consumption vs. production of animal source foods raises important ethical issues. Especially when fast growing poor populations are considered,

conserving natural areas is essential to ensure their ability to achieve higher levels of human development.

The Environmentally-adjusted Human Development Index (EHDI) we propose here represents a wider concept of human development, as (1) it is a more accurate predictor of human well-being than the current HDI, and (2) the environmental dimension accounts for the maintenance or depletion of the ecosystems that generate wealth expressed in the other dimensions. The adoption of the EHDI could be a powerful inducer of public policy, as governments would find themselves pressed to conserve natural land cover in their strive to increase their countries' development indices. Given the much higher efficiency of plant-based foods, promoting a transition to more plant-based diets, is a promising strategy to increase countries' EHDI. We hope our recommendations may help guiding governments and policy makers to act towards wilder and happier countries.

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Supplementary Material

Available at:

<https://drive.google.com/open?id=1ps8BrVhK3ecNRNgHwqAhGrNmoPgMhi83>

Table S1. Raw data used to build the candidate models. The overall life satisfaction index (OLSI), the Human Development Index (HDI) level, the HDI, and its four components (life expectancy at birth – LEB, expected years of schooling – EYS, mean years of schooling – MYS, and gross national income per capita – GNI) were obtained from the Human Development Report 2016. The EYS and GNI are capped at 18 years and \$75,000 per capita, respectively. The four components of the HDI were used to generate the health, education and income indices. Total pixels and natural land cover (NLC) pixels, which were obtained with the spatial analysis, were used to calculate the NLC percentage and index. Similarly, total land area and protected land area, which were obtained

from the World Database on Protected Areas, were used to calculate the protected land cover (PLC) percentage and index. The Environmentally-adjusted Human Development Index (EHDI) is given by the geometric mean of the health, education, income, and NLC indices. The development value correction was calculated by subtracting the HDI from the EHDI, and was used to build the map shown in Figure 2. The maximum and minimum corrections were 0.103 and – 0.296, respectively. The HDI rank, the EHDI rank, and the difference between them (development rank difference) are also given. For 31 of the 187 countries shown, the OLSI is not available (NA), and thus the model selection analysis considered the remaining 156 countries. All data refer to the year 2015.

Table S2. Coefficient estimates and *P*-values for the variables used in the generalized linear models to predict the overall life satisfaction index. All models were fitted using a Gamma family distribution and the inverse link function.

Table S3. Pearson's *r* coefficients and their *P*-values for each pair of indices used in the proposed Environmentally-adjusted Human Development Index.

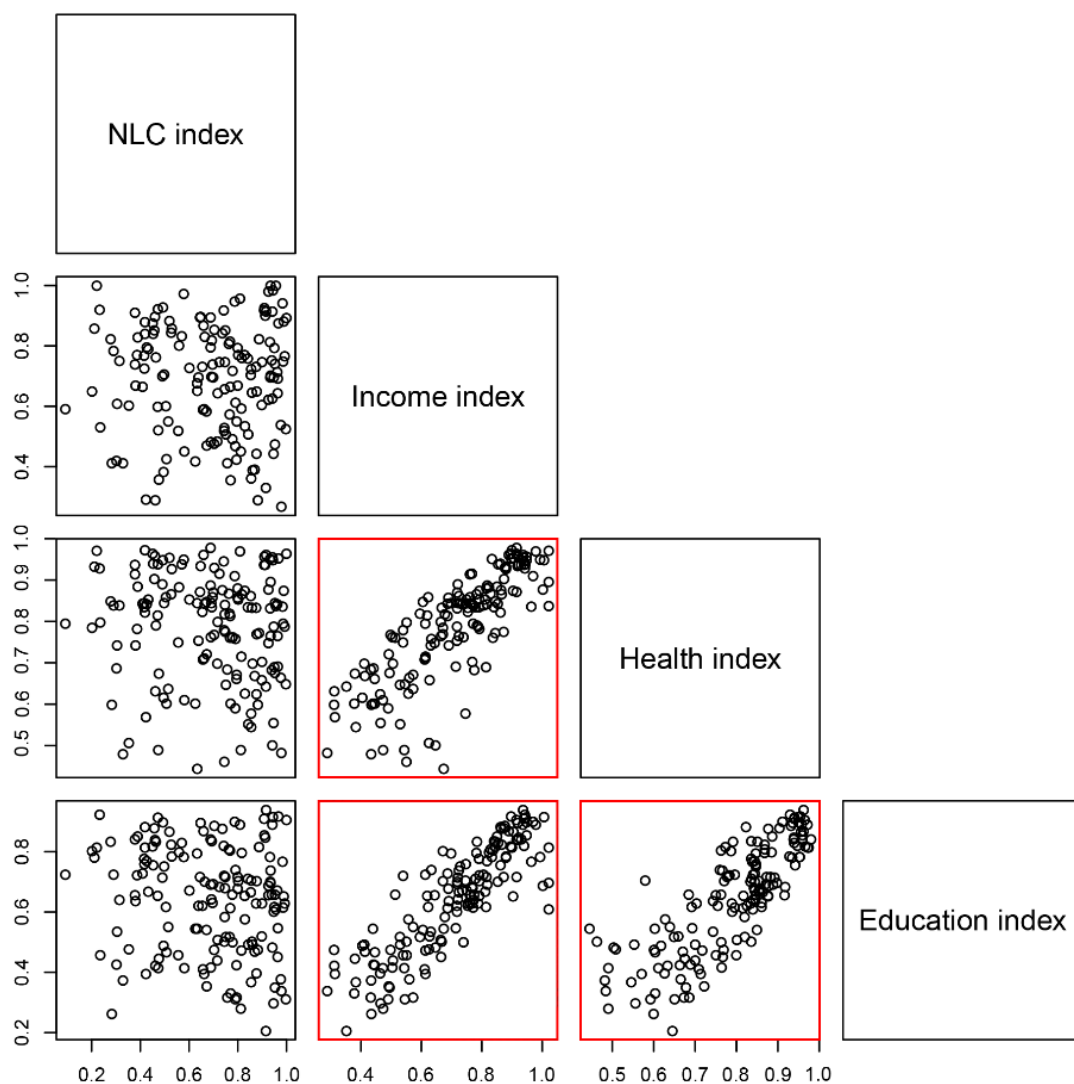


Figure S1. Correlation among the four variables considered in the selected model (OLSI \sim H + E + I + NLC). Significant correlations ($P < 0.05$) are shown within red borders. See Table S3 for detailed values.

CHAPTER 3

Changing diets to bring nature back and improve human development

Abstract

Habitat loss due to conversion to agriculture and related disruption of water, carbon and nutrients cycles and chemical pollution currently lead the ongoing biodiversity crisis worldwide. Moreover, their environmental impacts seriously threaten the provision of ecosystem services to human populations. Although approximately 70% of the global agricultural land is presently dedicated to produce animal-based foods, such as meat, dairy and eggs, these products represent mere 18% and 39% of global caloric and protein intake, respectively. The high consumption level of animal products is an established public health concern in developed countries, as it plays a critical role in the epidemics of non-communicable diseases. This situation is increasingly afflicting emerging economies, for higher incomes tend to create a demand for increased consumption of such foods. The environmental and health issues attributable to the production and consumption of animal products have led to explicit recommendations towards more plant-based diets. In this study, we estimate the agricultural area change in the world's countries under four scenarios of substitution of animal protein by vegetal protein, while maintaining current consumption, production, and international trade patterns of plant products. Because of the much lower land area required to produce plant-based foods when compared to animal products, substituting animal protein by vegetal protein has the potential to release from agriculture up to 3.1 billion ha globally, i.e., approximately 20% of global land area. In addition to the enormous benefits of

such land sparing to biodiversity conservation, the abandonment of agricultural land that would occur in most countries could be passively restored into natural land cover, improving these countries' Environmentally-adjusted Human Development Index. As wild caught fish and aquatic invertebrates are included in the replaced animal-based foods, substituting animal protein by vegetal protein also constitutes a great opportunity to alleviate the massive pressure human populations have exerted on freshwater and marine species. Our results reveal that a shift towards more plant-based diets is probably the single strategy most capable of simultaneously improving biodiversity conservation and human development aspirations.

Keywords: agricultural area, animal-based foods, animal products, dietary transition, ecological restoration, plant-based diets.

Introduction

From hot rainy tropical forests to cold dry tundra, our planet's surface has been covered with an immense variety of natural habitats for millions of years, each one with characteristic species assemblages (Olson *et al.*, 2001). A fundamental change in the way humans obtain food happened about 11 to 9 thousand years ago when, for the first time, hunting and gathering started being replaced by agriculture (Smith & Zeder, 2013). Ever since plants and animals were domesticated, and more strikingly since the industrial revolution, natural habitats have been converted into croplands, pastures, and human settlements, together currently accounting for approximately 39% of all ice-free land area (Ellis *et al.*, 2010). Habitat alteration caused by land-use change and related pressures is the

number one proximate cause of worldwide biodiversity crisis (Ducatez & Shine, 2016) which, for its exceptional rate of species extirpation, has been considered the sixth mass extinction in the planet's history (Kolbert, 2014; Ceballos *et al.*, 2015). While temperate regions had suffered severe land-use change in past centuries, deforestation currently happens mainly in tropical regions (Ellis *et al.*, 2010), where alarming species loss is expected to occur in the near future. For instance, Estrada *et al.* (2018) have predicted agriculture expansion during the 21st century will cause a contraction of 78% of primate habitats in Brazil, 72% in Indonesia, 62% in Madagascar, and 32% in the Democratic Republic of the Congo, four tropical countries harboring 65% of the world's primate species. Massive conversion of natural habitats into agricultural areas, which inevitably happens at the expense of the Earth's biodiversity and life-support system, is expected to further increase to keep pace with the growing human population and increasing demand for animal-based foods (Kearney, 2010; Tilman *et al.*, 2011, Alexandratos & Bruinsma, 2012; Kastner *et al.*, 2012; Weinzettel *et al.*, 2013).

Along with the negative consequences to other species, the loss of natural habitats also poses serious threats to our species, as we depend on the many and intricate ways by which nature promotes both the well-being and prosperity of human populations. This can be illustrated by the plurality of ecosystem services provided to humans, like food, water, raw materials, climate regulation, soil maintenance, and pollination, among many others (Costanza *et al.*, 1997; de Groot *et al.*, 2012; Costanza *et al.*, 2014). The experience of nature also delivers multiple benefits to humans, such as physical, psychological, and social ones (Keniger *et al.*, 2013; Shanahan *et al.*, 2016a; Shanahan *et al.*, 2016b). The benefits of nature to humans are detectable not only at local level, but also at

country level. The socioeconomic factors being identical, the population of a country with a higher percentage of natural land cover reports higher values of overall life satisfaction than a country with a lower percentage of its territory covered by natural habitats (Chapter 2 of this thesis).

It is important to acknowledge that different human populations are not equally affected by global environmental changes like land conversion (Newbold *et al.*, 2015; Prell *et al.*, 2017). Tropical regions, which are mostly occupied by developing countries, currently face a 62% acceleration in net deforestation (Kim *et al.*, 2015), largely driven by the demand of agricultural commodities by developed countries (Naylor *et al.*, 2005; Lenzen *et al.*, 2012). As a higher proportion of temperate ecosystems, where most rich countries are located, was previously converted into agricultural land (Ellis *et al.*, 2010), the high consumption levels of their inhabitants tend to cause land-use change outside their borders. Moreover, nations that are more affluent have the conditions to push highly impacting agricultural activities to other countries with more available area and/or weaker restrictions (Lenzen *et al.*, 2012; Weinzettel *et al.*, 2013). Especial attention is needed to halt environmental degradation in developing countries. Otherwise, the degradation of biodiversity, climate, soil, and water quality might compromise the ability of those populations to achieve desirable levels of human development. In the interest of all biodiversity and our own species, it is critical to understand how our present convenience to use nature's resources might undermine the basic needs of generations to come, especially the poorest ones (Sanderson *et al.*, 2002; Foley *et al.*, 2005; Godfray *et al.*, 2010; Foley *et al.*, 2011; de Groot *et al.*, 2012).

Food production is the major single cause of land-use change (Wilting *et al.*, 2017), of which 70% is driven by the production of animal-based foods (Steinfeld *et al.*, 2006). Indeed, recent studies have found dietary preferences to be the most important determinant of agricultural land requirement (Alexander *et al.*, 2016; Donati *et al.*, 2016; Erb *et al.*, 2016a). The livestock sector accounts for 8% of global human use of freshwater, and it is probably the major source of water pollution through the excessive production of nutrients, sediments, agrochemicals, antibiotics and hormones. When released in the environment, these substances have dire impacts on freshwater and marine ecosystems, as well as on human health (Tilman *et al.*, 2002; Islam & Tanaka, 2004; Camargo & Alonso, 2006; Steinfeld *et al.*, 2006; Diaz & Rosenberg, 2008). Due to the release of methane from enteric fermentation, nitrous oxide from manure and fertilizer, and carbon dioxide from land-use change and agricultural energy use, among other factors, the livestock sector is also responsible for the emission of 7.1 gigatonnes of carbon dioxide-equivalent per year, which represents 14.5% of all human-induced greenhouse gases emissions (Gerber *et al.*, 2013). This number increases to 74% if only the global food production system is considered (Davis *et al.*, 2016), which is in accordance with the well-known fact that the production of animal-based foods is much less efficient than the production of their vegetal equivalents. This is true not only for the most impacting animal-based foods, like meat from ruminant animals (cattle, sheep, and goats), which is characterized by having an impact 20-100 times that of plant-based foods when greenhouse gasses emission, land use, energy use, acidification and eutrophication potential are considered in life cycle assessments (Nijdam *et al.*, 2012; Davis *et al.*, 2016; Clark & Tilman, 2017). The lowest-impact animal products also typically perform

worse than vegetal alternatives in terms of environmental burden (Alexander *et al.*, 2016; Gephart *et al.*, 2016; Clark & Tilman, 2017; Poor & Nemecek, 2018). About 70% of global agricultural land and 36% of global ice-free land surface is dedicated to the production of animal-based foods alone (Steinfeld *et al.*, 2006; Erb *et al.*, 2016b), and 43-87% of an individual's environmental footprint is due to the consumption of animal products (Davis *et al.*, 2016). However, these foods represent mere 18% and 39% of caloric and protein intake (Davis *et al.*, 2016). We live in a world where approximately one-third of global arable land is allocated to grow grains and other crops to feed livestock (Steinfeld *et al.*, 2006; Cassidy *et al.*, 2013), and where the highest loss rates (81-94%) of global agricultural net primary production are associated with livestock production (Alexander *et al.*, 2017). This situation generates an increasing concern about the competition between food and feed crops, as this has the potential to seriously compromise the ability of the global food system to nurture the growing human population in the next decades (Smith *et al.*, 2013; Bajželj *et al.*, 2014; Ripple *et al.*, 2014; Davis & D'Odorico, 2015; Di Paola *et al.*, 2017).

Not surprisingly, recommendations of dietary shifts towards more plant-based diets have started to rise as an indispensable strategy to curb agriculture-related environmental impacts and guarantee food security (Steinfeld *et al.*, 2006; Cassidy *et al.*, 2013; Hedenus *et al.*, 2014; Billen *et al.*, 2015; Machovina *et al.*, 2015; Wellesley *et al.*, 2015; Davis & D'Odorico, 2015; Gephart *et al.*, 2016; Visconti *et al.*, 2016; Alexander *et al.*, 2017; Clark & Tilman, 2017; Willett *et al.*, 2019). Although opportunities exist in production/supply-side measures, such as increasing productivity and reducing waste (Godfray & Garnett, 2014; Clark & Tilman, 2017; Rööß *et al.*, 2017), these strategies are often found to be

insufficient to deliver the desired environmental and food security outcomes (Garnett *et al.*, 2013; Smith *et al.*, 2013; Davis *et al.*, 2016; Springmann *et al.*, 2018). On the other hand, consumption/demand-side approaches, essentially composed by dietary changes, are increasingly found to be more promising strategies to achieve those goals (Popp *et al.*, 2010; Alexander *et al.*, 2016; Poore & Nemecek, 2018). Among all diets, the strictly plant-based (vegan) diet has consistently been found to have the highest potential to reduce environmental impact (Stehfest *et al.*, 2009; Berners-Lee *et al.*, 2012; Baroni *et al.*, 2014; Hallstrom *et al.*, 2015; Erb *et al.*, 2016a; Rööß *et al.*, 2017). Despite concerns with human nutritional requirements (e.g., Ridoutt & Hendrie, 2017), mounting evidence indicates plant-based diets are appropriate and beneficial to humans (e.g., Craig *et al.*, 2009; Clarys *et al.*, 2014; Schüpbach *et al.*, 2015).

In addition to the environmental benefits of a dietary change, a reduction of animal-based foods' consumption accompanied by an increase in fruits, vegetables, and whole grains would result in outstanding improvements of human population's health (Scarborough *et al.*, 2012; Tilman & Clark, 2014; Westhoek *et al.*, 2014; Briggs *et al.*, 2016; Etemadi *et al.*, 2017). Indeed, lower incidence of diabetes, cardiovascular diseases, and cancer, among other non-communicable diseases, have consistently been observed in vegetarians and vegans when compared to omnivores (Key *et al.*, 2014; Le & Sabaté, 2014; Dinu *et al.*, 2017). As a pandemic of non-communicable diseases has been a serious issue of public health in developed and developing countries (Daar *et al.*, 2007; Beaglehole *et al.*, 2011; WHO, 2017), the ecology-oriented recommendations to reduce the consumption of animal-based foods thus represent a great opportunity to tackle global health issues as well, with profound benefits for overall human well-being.

In this study we estimated (1) the agricultural area change in the world's countries under scenarios of 25%, 50%, 75%, and 100% substitution of animal protein by vegetal protein, (2) the consequent natural land cover (NLC) area change, and (3) countries' Environmentally-adjusted Human Development Index (EHDI) considering that such NLC area change is added to the existing NLC.

Methods

In our simulations, we assume that all countries would adopt the same proportion of protein substitution simultaneously. Some territories (French Polynesia, Hong Kong, Macau, New Caledonia, and Taiwan) were also included, but here we refer to them as countries as well, for the sake of simplicity. To assess the agricultural area change in each country, we first needed to calculate: (1) the area allocated to produce animal products (AP), which is the sum of the area of permanent meadows and pastures and the area allocated to produce feed, independently of these crops being used as feed in the country of production or exported to serve as feed in importing countries; (2) the area allocated to produce plant products (PP), also independently of where they are consumed; and (3) the area needed to replace animal protein by vegetal protein. The agricultural area change was given by subtracting the area allocated to produce animal products from the area needed to replace animal protein.

We used the online database of the United Nations' Food and Agriculture Organization (FAO, 2018b) as our main data source. Within this source, (1) production, import, stock variation, export, domestic supply quantity, food, feed, other uses, processing, seed, and losses data for each food item in each country were obtained from the Food Balance Sheet domain (FBS), as well as food

supply quantity and protein supply quantity from vegetal products and from all products (grand total) for each country and the world; (2) yield and harvested area data for each crop in each country were obtained from the Crops domain (QC); (3) country area, agricultural area, and Permanent meadows and pastures area for each country were obtained from the Land Use domain (RL); (4) herbaceous crops and woody crops area were obtained from the Land Cover domain (LC). The total population data were obtained from the United Nations' Population Division (United Nations, 2017).

All data refer to the year 2013, except for the item “oats” in Japan. In this case, as the quantities appeared inexplicably negative for the years 2013 and 2012, we assumed there was an error when constructing the database, and we used 2011 data. Similarly, as the processing quantity of “fruits, other” item in Uzbekistan was negative (-4 thousand tonnes), and because data from 2009 to 2013 consistently reported small values, we considered it a negligible error and fixed this value in zero. We also standardized all the units in the original datasets into tonnes, ha, tonnes per ha, per capita, and tonnes per capita per year (see analysis code in SM for details).

From the Food Balance Sheet, we considered 44 majors agricultural crops that represent more than 90% of global calorie production (Table S1; Monfreda *et al.*, 2008). The food items in the FBS refer to a specific crop and its products (e.g., apples and food products derived from apples), and sometimes to more than one crop and their products (e.g., other vegetables include asparagus and spinach and their products, among others). As the data in Crops domain refer to single crops, we followed the definition of each food item in FBS to create a correspondence between QC crops and FBS food items (Table S1). The yield of

a food item composed by more than one crop was calculated considering the yield of those crops and their relative contribution to the food item in each country. For the sake of simplicity, from now on we use the term crop to refer to items in both FBS and QC domains.

Area allocated to produce animal products and plant products

After careful examination of the Food Balance Sheet data, as well as FAO's definitions, we concluded the domestic supply quantity (DSQ) of each crop is supposed to equal both PIES (production + import + stock variation - export) and PLOSFF (food + feed + other uses + processing + seed + losses). However, we detected some country-crop combinations presented discrepancies between the values of DSQ, PIES, and PLOSFF. Also, for some of them, DSQ and PIES had negative values. Because PLOSFF produced no negative values, we (1) replaced the original DSQ by the PLOSFF value, and (2) replaced the value of each PIES component to make PIES equal to PLOSFF (and to the new DSQ), while maintaining the original proportions of PIES components. This operation was performed for the entire FBS dataset.

We also concluded the export quantity originates from production, import, and stock variation. By its turn, stock variation necessarily comes from the two ultimate forms of input: production and import. Having this in mind, we assumed: (1) production, import, and stock variation are exported according to their relative proportions; (2) production, import, stock variation and export are processed according to their relative proportions; (3) processing of non-oil crops generates food, feed, and ingredients for other uses according to their relative proportions of unprocessed quantity (when no unprocessed quantity exists, the quantity of

processed non-oil crop was equally divided among food, feed, and other uses); (4) the oil content of the seven oil crops (Table S2) is processed into equal proportions of food and other uses, while the solid content is processed into feed; (5) seed is used to grow crops to produce food, feed, and other uses according to their relative proportions; and (6) losses come from substance formerly destined to food, feed, and other uses following their relative proportions (Figure 1).

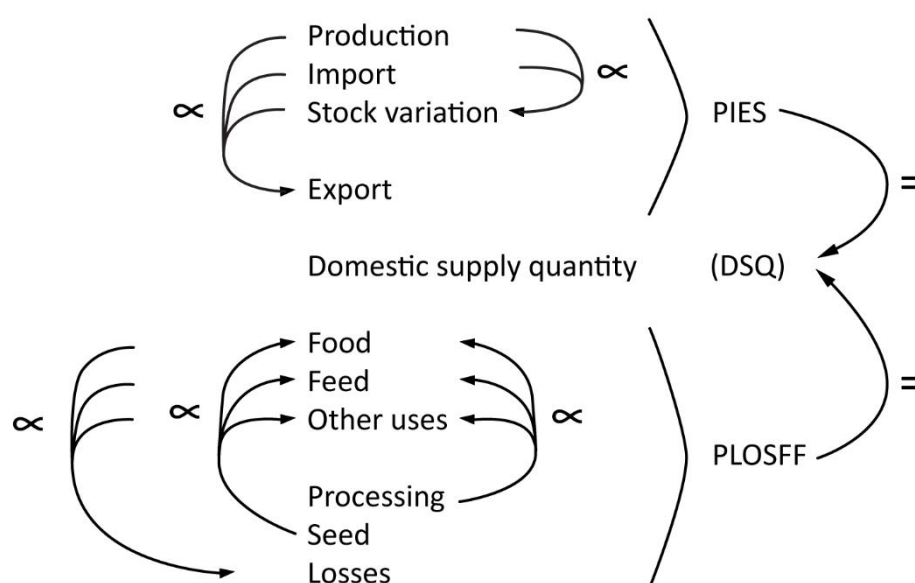


Figure 1. Relationships between production, import, stock variation, export, domestic supply quantity, food, feed, other uses, processing, seed, and losses in FAO's Food Balance Sheet.

Based on the assumptions described above, we created the following basic proportions: of input to export, of input to domestic use, of DSQ that is unprocessed, of DSQ that is unprocessed feed, of DSQ that is unprocessed food, of DSQ that is processed feed, of DSQ that is processed food, of DSQ that is seed to produce feed, of DSQ that is seed to produce food, of DSQ that is losses

from feed, of DSQ that is losses from food. We also estimated the weight of each country's export in the global export quantity of each crop.

We multiplied the already known quantities of production, import, and stock variation by the required combination of those basic proportions to calculate the following quantities of each crops in each country: nationally produced unprocessed feed to domestic use, nationally produced processed feed to domestic use, nationally produced unprocessed to export for feed, nationally produced processed feed to export, nationally produced seed to produce feed to domestic use, nationally produced seed to export to produce feed, losses from nationally produced feed to domestic use, and losses from nationally produced feed to export. We followed the same rationale to assess the food-related versions of those quantities (e.g., nationally produced unprocessed food to domestic use). For a given crop in a given country, the sum of these quantities divided by their respective yield gives the area occupied by the quantity of that crop that is used as feed. The sum of this area for all crops gives the total area allocated for feed in that country. The area allocated to produce plant-based foods was calculated following exactly the same rationale as the area allocated to produce feed, but using the food-related versions of those quantities instead (e.g., nationally produced unprocessed food to domestic use; see analysis code in SM for details).

The area of permanent meadows and pastures (PMP; the land used permanently – for a period of five years or more – for herbaceous forage crops, either cultivated or naturally growing; FAO, 2018b) in each country was summed to the area allocated for feed to obtain the area allocated to produce animal products. For the seven countries to which no PMP area was available (Table

S3), we produced a conservative adjusted value by subtracting agricultural area from the sum of herbaceous and woody crops. When this operation produced a negative value, which happened in the case of Bermuda, we fixed PMP as zero (Table S3).

Area needed to replace animal protein by vegetal protein

We calculated the quantity of protein to replace in each country by subtracting the total vegetal protein supply quantity (the sum of protein supply quantity from all the 44 crops) from the grand total (animal and vegetal) protein supply quantity. The quantity of protein to replace includes both protein from wild animals (both aquatic and terrestrial, which are obtained independently of agricultural land) and protein from farmed animals (whose production requires agricultural land), as it is impossible to disentangle the wild and farmed origin of animal protein using the FBS.

For the 39 countries with a grand total protein supply quantity value lower than 63 g per capita per day (Table S3), we adjusted this value to 63. The value of 63 g per capita per day was conservatively calculated considering (1) the recommended daily protein intake of 0.83 g per kg of healthy body weight (Millward, 2012); and (2) a body weight of 75 kg, which produces an adequate body mass index for a person of up to 2 meters of height (WHO, 2018). This way, besides the goal of sparing agriculture area, we also assured no country would have protein deficiency after the substitution. In countries where the protein quantity per capita per day exceeded 63 g, we maintained the original value.

To calculate the quantity of each crop to replace in each country, we multiplied the quantity of protein to replace by the proportion of each crop in the

total vegetal protein supply quantity, and then divided the result by the crop protein content. By using the proportion of each crop in the total vegetal protein supply quantity, we avoid unnecessary change in countries' plant-based foods consumption patterns. Protein content of each crop was obtained by dividing protein supply quantity by food supply quantity for the world data (Table S1).

Based on the food-related quantities calculated to assess the area allocated to produce plant-based foods, we assessed the proportion of food supply that comes from national production, as well as from import. We used national production and import proportions to determine the amount of each replacement crop that should be nationally produced and imported (and consequently exported), guaranteeing the replacement crops would not alter market relations between countries, nor countries' production patterns. Using seed-food and losses-food ratios, we also considered the additional seed and losses associated with replacing crops. In this computation, the nationally produced and imported proportions were also applied.

The total replacement area in each country was given by the sum of all replacement crops after divided by their respective yield. It included replacement crops to domestic use as well as to export. Replacement crops' quantity to export were calculated by multiplying the global quantity of each replacement crop by the current weight of each country's export in the global export, and then divided by their respective yield.

Given the complexity of the database and of the calculations needed to assess the required intermediate steps, we have generated several coherence tests along the process. These tests allowed us to confirm no inconsistencies regarding the previously described assumptions occurred. As the values in FAO's

Food Balance Sheet are rounded to the nearest thousand by default, differences of up to 1,000 were due to a rounding error and were thus considered negligible). These coherence tests are included in the analysis code itself. In order to built more robust coherence tests, all the calculations performed to feed and food were also made for other uses (see analysis code in SM for details).

Agricultural area change

We obtained the agricultural area change for each country by subtracting the area allocated to produce animal-based foods from the area needed to replace animal protein by vegetal protein. As all the calculations previously described were performed considering the 100% substitution scenario, we multiplied the result of this subtraction by 0.75, 0.5, and 0.25 to assess the agricultural area change in the 75%, 50%, and 25% substitution scenarios. Negative values of agricultural area change indicate less agricultural area than currently used would be needed after protein substitution, and could thus be converted back into natural land cover. Positive values of agricultural area change indicate more agricultural area would be needed for food production after protein substitution, which would imply further conversion of natural habitats into agricultural lands.

Natural land cover area change

Following the rationale described in the previous paragraph, the NLC area change was given by the additive inverse (i.e., what you add to a number to get zero) of the agricultural area change. In addition to calculating the total NLC area change for each country included in the analysis, we also calculated the area change for the six NLC categories presented in FAO's LC domain that are

suitable to be converted into agricultural land: tree-covered areas; shrub-covered areas; grassland; shrubs and/or herbaceous vegetation, aquatic or regularly flooded; mangroves; and sparsely natural vegetated areas. This was made by multiplying the NLC area change in each country by the relative proportion of each one of these six land cover categories as in 2013.

The effect of protein substitution on the EHDI

The EHDI is given by the geometric mean of the environmental, health, education, and income indices for each country (Chapter 2 of this thesis). The health, education and income indices for the year 2013 were obtained from the United Nation's development report (United Nations, 2014). To estimate each country's NLC as in 2013, we subtracted the agricultural area and the area of artificial surfaces from the total country area. The area of artificial surfaces (including urban and associated areas) was obtained from FAO's LC domain. To the 2013 NLC, we summed the NLC change under each one of the four protein substitution scenarios, which produced four projected NLC values for each country. These four projected NLC values were divided by respective total country area to produce the NLC indices, which were then used as the environmental dimension of the projected EHDI.

Results

Our results show that an estimated total of 3,101,530,906 ha would globally be freed from agriculture in the scenario of 100% substitution of animal protein by vegetal protein (Tables 1 and 2), distributed approximately as 31% for forests, 27% for grasslands, 22% for shrub lands, 19% for sparse vegetation, 1% for

flooded vegetation, and 0.1% for mangroves (Table 2). Protein substitution results in a decrease of agricultural area for 142 (82%) of the 173 countries included in the analysis, while it implies some agricultural area increase in the remaining 31 countries (Table 1; Figure 2). In the former 142 countries, the area that could be restored into NLC totals 3,139,885,111 ha, a value approximately 82 times larger than the NLC area that would be further lost to agriculture in those 31 countries (38,354,205 ha) (Tables 1 and 2). Considering all the 173 countries in the 100% protein substitution scenario, the mean relative agricultural area change (i.e., the agricultural area change divided by total country area) is -17% (Table 1). If we consider only the countries where protein substitution has a positive effect, the mean agricultural area change is -23% (Table 1), varying from less than -0.5% for Saint Kitts and Nevis ^{Note 1} to -79% for Saudi Arabia (Table S4). These values are considerably lower in the group of countries where some extra area would be needed to produce vegetal protein, which lose on average 10% of their total area (Table 1), varying from <0.5% for Suriname to 62% for Hong Kong (Table S4).

Considering the 173 countries and the 44 crops included in the analysis, we estimated the global agricultural area in 2013 to be 4,392,555,484 ha. The areas allocated to produce crops to feed livestock and plant-based foods represented 34% and 58% of all crops area, respectively. The areas allocated to produce animal and plant products represented respectively 73% and 15% of global agricultural land area (Table S5).

Table 1. The agricultural area change (AAC) and the relative agricultural area change (RAAC – the proportion of AAC in relation to respective country area) under four scenarios of substitution of animal protein by vegetal protein. Absolute areas are given in ha and are rounded to the nearest integer. Values for all 173 countries are presented in Table S4. * Data for China do not include Hong Kong, Macao, nor Taiwan.

		Substitution scenarios								
		100%		75%		50%		25%		
		AAC	RAAC	AAC	RAAC	AAC	RAAC	AAC	RAAC	
Summary	Total of all (173) countries	-3101530906	-24.7%	-2326148179	-18.5%	-1550765453	-12.3%	-775382726	-6.2%	
	Mean of all (173) countries	-17927924	-17.4%	-13445943	-13.1%	-8963962	-8.7%	-4481981	-4.4%	
	Total of countries with negative AAC (142)	-3139885111	-26.3%	-2354913833	-19.7%	-1569942556	-13.2%	-784971278	-6.6%	
	Mean of countries with negative AAC (142)	-22111867	-23.5%	-16583900	-17.6%	-11055933	-11.7%	-5527967	-5.9%	
	Total of countries with positive AAC (31)	38354205	6.0%	28765654	4.5%	19177103	3.0%	9588551	1.5%	
	Mean of countries with positive AAC (31)	1237232	10.3%	927924	7.7%	618616	5.2%	309308	2.6%	
Ranking by AAC	Top 10 countries	China*	-381499433	-39.9%	-286124575	-29.9%	-190749716	-19.9%	-95374858	-10.0%
		Australia	-350965377	-45.3%	-263224033	-34.0%	-175482688	-22.7%	-87741344	-11.3%
		United States	-268362453	-27.3%	-201271840	-20.5%	-134181227	-13.6%	-67090613	-6.8%
		Brazil	-210927868	-24.8%	-158195901	-18.6%	-105463934	-12.4%	-52731967	-6.2%
		Kazakhstan	-182459080	-67.0%	-136844310	-50.2%	-91229540	-33.5%	-45614770	-16.7%
		Saudi Arabia	-169475801	-78.8%	-127106851	-59.1%	-84737900	-39.4%	-42368950	-19.7%
		Argentina	-123873950	-44.6%	-92905463	-33.4%	-61936975	-22.3%	-30968488	-11.1%
		Mongolia	-112441610	-71.9%	-84331207	-53.9%	-56220805	-35.9%	-28110402	-18.0%
		Russian Federation	-95591245	-5.6%	-71693434	-4.2%	-47795622	-2.8%	-23897811	-1.4%
		South Africa	-84179025	-69.1%	-63134269	-51.8%	-42089513	-34.5%	-21044756	-17.3%
	Bottom 10 countries	Sri Lanka	464712	7.1%	348534	5.3%	232356	3.5%	116178	1.8%
		Taiwan	501738	14.0%	376303	10.5%	250869	7.0%	125434	3.5%
		Japan	1041792	2.8%	781344	2.1%	520896	1.4%	260448	0.7%
		Republic of Korea	1398454	13.9%	1048840	10.5%	699227	7.0%	349613	3.5%
		Philippines	2431972	8.1%	1823979	6.1%	1215986	4.1%	607993	2.0%
		Viet Nam	3490823	10.5%	2618117	7.9%	1745412	5.3%	872706	2.6%
		Pakistan	3829504	4.8%	2872128	3.6%	1914752	2.4%	957376	1.2%
		Bangladesh	3995108	26.9%	2996331	20.2%	1997554	13.5%	998777	6.7%
		Thailand	4503383	8.8%	3377537	6.6%	2251691	4.4%	1125846	2.2%
		India	15537161	4.7%	11652871	3.5%	7768581	2.4%	3884290	1.2%
Ranking by RAAC	Top 10 countries	Saudi Arabia	-169475801	-78.8%	-127106851	-59.1%	-84737900	-39.4%	-42368950	-19.7%
		Djibouti	-1692743	-73.0%	-1269557	-54.7%	-846371	-36.5%	-423186	-18.2%
		Mongolia	-112441610	-71.9%	-84331207	-53.9%	-56220805	-35.9%	-28110402	-18.0%
		Uruguay	-12338007	-70.0%	-9253505	-52.5%	-6169003	-35.0%	-3084502	-17.5%
		South Africa	-84179025	-69.1%	-63134269	-51.8%	-42089513	-34.5%	-21044756	-17.3%
		Kazakhstan	-182459080	-67.0%	-136844310	-50.2%	-91229540	-33.5%	-45614770	-16.7%
		Turkmenistan	-31785057	-65.1%	-23838793	-48.8%	-15892529	-32.6%	-7946264	-16.3%
		Lesotho	-1952049	-64.3%	-1464037	-48.2%	-976024	-32.1%	-488012	-16.1%
		Madagascar	-35696445	-60.8%	-26772333	-45.6%	-17848222	-30.4%	-8924111	-15.2%
		Swaziland	-1005453	-57.9%	-754089	-43.4%	-502726	-29.0%	-251363	-14.5%
	Bottom 10 countries	Haiti	309563	11.2%	232173	8.4%	154782	5.6%	77391	2.8%
		Samoa	33814	11.9%	25361	8.9%	16907	6.0%	8454	3.0%
		Saint Lucia	8530	13.8%	6398	10.3%	4265	6.9%	2133	3.4%
		Republic of Korea	1398454	13.9%	1048840	10.5%	699227	7.0%	349613	3.5%
		Taiwan	501738	14.0%	376303	10.5%	250869	7.0%	125434	3.5%
		Grenada	5270	15.5%	3953	11.6%	2635	7.8%	1318	3.9%
		Malta	8123	25.4%	6092	19.0%	4062	12.7%	2031	6.3%
		Maldives	7632	25.4%	5724	19.1%	3816	12.7%	1908	6.4%
		Bangladesh	3995108	26.9%	2996331	20.2%	1997554	13.5%	998777	6.7%
		Hong Kong	68332	62.1%	51249	46.6%	34166	31.1%	17083	15.5%

Table 2. The natural land cover area change (NLCAC) and the relative natural land cover area change (RNLCAC – the proportion of NLCAC in relation to respective country area) under the 100% substitution scenario of animal protein by vegetal protein. Absolute and relative distribution of NLCAC among the following six natural land cover (NLC) categories are also given: tree-covered areas (Tree), shrub-covered areas (Shrb), grassland (Gras), sparsely natural vegetated areas (Spar), aquatic or regularly flooded areas (Floo), and mangroves (Mang). This distribution follows the relative proportion of the NLC categories in each country as in 2013. Areas are given in ha and are rounded to the nearest integer. Values for all 173 countries and the 75%, 50%, and 25% substitution scenarios are presented in Table S6. * Data for China do not include Hong Kong, Macao, nor Taiwan.

				NLC categories												
				Tree		Shrb		Gras		Spar		Floo		Mang		
				absolute	relative	absolute	relative	absolute	relative	absolute	relative	absolute	relative	absolute	relative	
Summary	Total of all (173) countries	3101530906	24.7%	967126504	31.2%	665634801	21.5%	826417842	26.6%	595580795	19.2%	42640629	1.4%	4130335	0.1%	
	Mean of all (173) countries	17927924	24.7%	5590327	31.2%	3847600	21.5%	4776982	26.6%	3442664	19.2%	246478	1.4%	23875	0.1%	
	Total of countries with positive NLCAA (142)	3139885111	26.3%	986043159	31.4%	674846935	21.5%	835238384	26.6%	596055875	19.0%	42889249	1.4%	4811510	0.2%	
	Mean of countries with positive NLCAA (142)	22111867	26.3%	6943966	31.4%	4752443	21.5%	5881960	26.6%	4197577	19.0%	302037	1.4%	33884	0.2%	
	Total of countries with negative NLCAA (31)	-38354205	-6.0%	-18916655	49.3%	-9212133	24.0%	-8820542	23.0%	-475080	1.2%	-248620	0.6%	-681175	1.8%	
	Mean of countries with negative NLCAA (31)	-1237232	-6.0%	-610215	49.3%	-297166	24.0%	-284534	23.0%	-15325	1.2%	-8020	0.6%	-21973	1.8%	
Ranking by NLCAC	Top 10 countries	China*	381499433	39.9%	134393786	35.2%	22713691	6.0%	206089249	54.0%	15863150	4.2%	2315978	0.6%	123579	0.0%
		Australia	350965377	45.3%	40321380	11.5%	92886686	26.5%	66335084	18.9%	144930861	41.3%	5131431	1.5%	1359935	0.4%
		United States	268362453	27.3%	110627910	41.2%	75069346	28.0%	72677948	27.1%	7071102	2.6%	2840597	1.1%	75551	0.0%
		Brazil	210927868	24.8%	135321135	64.2%	47891378	22.7%	23170578	11.0%	45825	0.0%	4304619	2.0%	194332	0.1%
		Kazakhstan	182459080	67.0%	10638812	5.8%	22795360	12.5%	86672530	47.5%	61155894	33.5%	1196484	0.7%	0	0.0%
		Saudi Arabia	169475801	78.8%	5255773	3.1%	11424829	6.7%	3684992	2.2%	148870378	87.8%	182329	0.1%	57499	0.0%
		Argentina	123873950	44.6%	22026331	17.8%	59333060	47.9%	9510745	7.7%	27580929	22.3%	5421917	4.4%	968	0.0%
		Mongolia	112441610	71.9%	12678785	11.3%	4036097	3.6%	46639248	41.5%	48566573	43.2%	520907	0.5%	0	0.0%
		Russian Federation	95591245	5.6%	63159454	66.1%	8698108	9.1%	10684458	11.2%	7685739	8.0%	5363487	5.6%	0	0.0%
		South Africa	84179025	69.1%	6955757	8.3%	50796669	60.3%	19014057	22.6%	7167693	8.5%	207753	0.2%	37095	0.0%
	Bottom 10 countries	Sri Lanka	-464712	-7.1%	-229066	49.3%	-160944	34.6%	-71301	15.3%	-896	0.2%	-4	0.0%	-2499	0.5%
		Taiwan	-501738	-14.0%	-449468	89.6%	-15727	3.1%	-22655	4.5%	-861	0.2%	-7884	1.6%	-5142	1.0%
		Japan	-1041792	-2.8%	-943737	90.6%	-41514	4.0%	-53299	5.1%	-150	0.0%	-2985	0.3%	-107	0.0%
		Republic of Korea	-1398454	-13.9%	-1195339	85.5%	-87408	6.3%	-101445	7.3%	-12468	0.9%	-1792	0.1%	0	0.0%
		Philippines	-2431972	-8.1%	-1669910	68.7%	-272273	11.2%	-382961	15.7%	-21978	0.9%	0	0.0%	-84850	3.5%
		Viet Nam	-3490823	-10.5%	-1941830	55.6%	-1101865	31.6%	-400643	11.5%	-1079	0.0%	-11342	0.3%	-34064	1.0%
		Pakistan	-3829504	-4.8%	-404438	10.6%	-914142	23.9%	-2146354	56.0%	-321038	8.4%	-42621	1.1%	-910	0.0%
		Bangladesh	-3995108	-26.9%	-1310593	32.8%	-1272814	31.9%	-944611	23.6%	-1515	0.0%	-36593	0.9%	-428983	10.7%
		Thailand	-4503383	-8.8%	-2355459	52.3%	-1220062	27.1%	-849587	18.9%	-5973	0.1%	-2517	0.1%	-69785	1.5%
		India	-15537161	-4.7%	-7730693	49.8%	-4030756	25.9%	-3561888	22.9%	-70431	0.5%	-95674	0.6%	-47719	0.3%

Table 2. Continued.

			NLC categories													
			NLCAC	RNLCAC	Tree		Shrb		Gras		Spar		Floo		Mang	
					absolute	relative	absolute	relative	absolute	relative	absolute	relative	absolute	relative	absolute	relative
Ranking by RNLCAC	Top 10 countries	Saudi Arabia	169475801	78.8%	5255773	3.1%	11424829	6.7%	3684992	2.2%	148870378	87.8%	182329	0.1%	57499	0.0%
		Djibouti	1692743	73.0%	18250	1.1%	174779	10.3%	472920	27.9%	350203	20.7%	671299	39.7%	5292	0.3%
		Mongolia	112441610	71.9%	12678785	11.3%	4036097	3.6%	46639248	41.5%	48566573	43.2%	520907	0.5%	0	0.0%
		Uruguay	12338007	70.0%	1796139	14.6%	637065	5.2%	9671517	78.4%	1089	0.0%	232197	1.9%	0	0.0%
		South Africa	84179025	69.1%	6955757	8.3%	50796669	60.3%	19014057	22.6%	7167693	8.5%	207753	0.2%	37095	0.0%
		Kazakhstan	182459080	67.0%	10638812	5.8%	22795360	12.5%	86672530	47.5%	61155894	33.5%	1196484	0.7%	0	0.0%
		Turkmenistan	31785057	65.1%	913600	2.9%	22215090	69.9%	4560197	14.3%	4091139	12.9%	4657	0.0%	374	0.0%
		Lesotho	1952049	64.3%	192177	9.8%	638876	32.7%	1120087	57.4%	154	0.0%	755	0.0%	0	0.0%
		Madagascar	35696445	60.8%	16371747	45.9%	6521062	18.3%	12450901	34.9%	40600	0.1%	198907	0.6%	113228	0.3%
		Swaziland	1005453	57.9%	568203	56.5%	192537	19.1%	237518	23.6%	239	0.0%	3621	0.4%	3335	0.3%
	Bottom 10 countries	Haiti	-309563	-11.2%	-59027	19.1%	-7677	2.5%	-200271	64.7%	-960	0.3%	-39762	12.8%	-1866	0.6%
		Samoa	-33814	-11.9%	-22924	67.8%	-4632	13.7%	-6124	18.1%	-3	0.0%	0	0.0%	-130	0.4%
		Saint Lucia	-8530	-13.8%	-8149	95.5%	-116	1.4%	-141	1.7%	-7	0.1%	-18	0.2%	-101	1.2%
		Republic of Korea	-1398454	-13.9%	-1195339	85.5%	-87408	6.3%	-101445	7.3%	-12468	0.9%	-1792	0.1%	0	0.0%
		Taiwan	-501738	-14.0%	-449468	89.6%	-15727	3.1%	-22655	4.5%	-861	0.2%	-7884	1.6%	-5142	1.0%
		Grenada	-5270	-15.5%	-4920	93.3%	-22	0.4%	-295	5.6%	0	0.0%	0	0.0%	-33	0.6%
		Malta	-8123	-25.4%	-3012	37.1%	-1630	20.1%	-2890	35.6%	-591	7.3%	0	0.0%	0	0.0%
		Maldives	-7632	-25.4%	-1701	22.3%	-2308	30.2%	-902	11.8%	-2683	35.2%	0	0.0%	-39	0.5%
		Bangladesh	-3995108	-26.9%	-1310593	32.8%	-1272814	31.9%	-944611	23.6%	-1515	0.0%	-36593	0.9%	-428983	10.7%
		Hong Kong	-68332	-62.1%	-52008	76.1%	-5794	8.5%	-8067	11.8%	-55	0.1%	-397	0.6%	-2011	2.9%

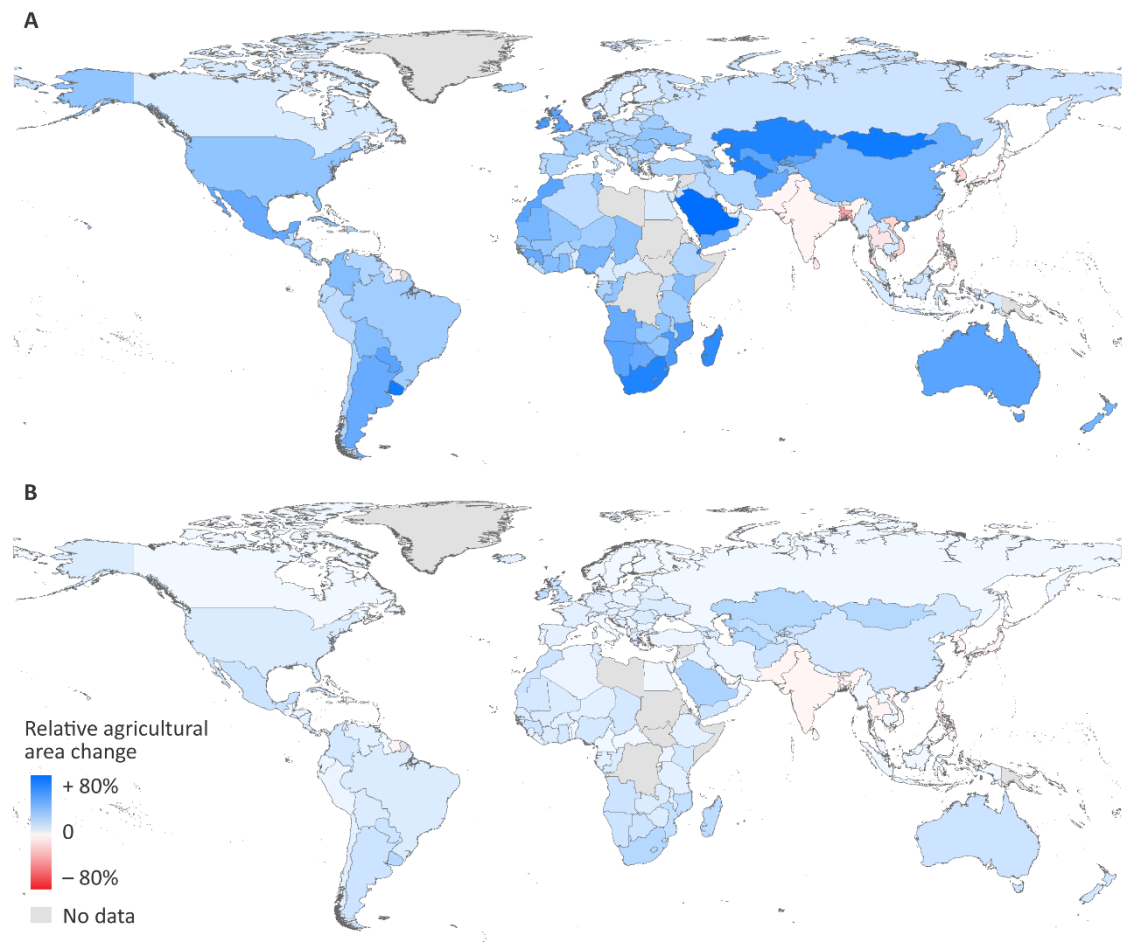


Figure 2. World maps showing the proportion of agricultural area change in relation to respective country area under scenarios of 100% (A) and 25% (B) of substitution of animal protein by vegetal protein. Blue tones indicate countries that gain area, i.e., where area is released from agriculture and made available to ecological restoration. Red tones indicate countries that lose area (where additional agricultural area would be required). The darker the color, the greater the change relatively to 2013 agricultural area. Note that the intensity of area loss never matches the intensity of area gain. See Table S4 for detailed values.

Considering the 100% substitution scenario for all 167 countries for which both the 2013 HDI and agricultural area change are available, the average increase of the EHDI in relation to 2013 EHDI is 7% (Table 3). For the 139 countries that would gain NLC area after protein replacement this value is 10% (varying from 50% for Saudi Arabia to <0.5% for Norway ^{Note 1}) (Table S7). As expected, all the 28 countries where the EHDI would decrease are among the countries for which protein replacement would require additional agricultural area. For these countries the average EHDI decrease is 5% in relation to 2013 EHDI (varying from <0.5% for Suriname to 30% for Hong Kong) (Table S7).

Table 3. Environmentally-adjusted Human Development Index (EHDI) values under four scenarios of substitution of animal protein by vegetal protein, as well as their respective proportional change in relation to the EHDI as in 2013. These estimations are based on the natural land cover area change produced by such substitution (see Table S6), and considering the Human Development Index (HDI) as in 2013. Values for all 167 countries are presented in Table S7.

		Substitution scenarios									
		HDI 2013	EHDI 2013	EHDI value	proportional change	EHDI value	proportional change	EHDI value	proportional change	EHDI value	proportional change
Summary	Mean of all (167) countries	0.690	0.656	0.703	7.1%	0.694	5.7%	0.683	4.1%	0.671	2.2%
	Mean of countries where the EHDI increases (139)	0.687	0.647	0.711	9.8%	0.698	7.8%	0.683	5.5%	0.667	3.0%
	Mean of countries where the EHDI decreases (28)	0.707	0.699	0.663	-5.2%	0.674	-3.6%	0.683	-2.3%	0.691	-1.1%
Top 10 countries	Saudi Arabia	0.836	0.579	0.870	50.2%	0.822	42.0%	0.765	32.1%	0.691	19.3%
	Uruguay	0.790	0.543	0.811	49.2%	0.767	41.2%	0.714	31.4%	0.645	18.8%
	South Africa	0.658	0.489	0.709	45.1%	0.672	37.5%	0.628	28.4%	0.571	16.7%
	Kazakhstan	0.757	0.545	0.785	44.0%	0.744	36.6%	0.695	27.6%	0.633	16.2%
	Djibouti	0.467	0.405	0.564	39.1%	0.536	32.3%	0.503	24.1%	0.462	14.0%
	Mongolia	0.698	0.553	0.762	37.9%	0.725	31.2%	0.681	23.2%	0.627	13.4%
	Lesotho	0.486	0.414	0.567	36.9%	0.540	30.3%	0.508	22.6%	0.468	13.0%
	Turkmenistan	0.698	0.569	0.756	33.0%	0.722	26.9%	0.681	19.9%	0.633	11.3%
	Madagascar	0.498	0.437	0.578	32.3%	0.552	26.4%	0.521	19.4%	0.485	11.0%
	Swaziland	0.530	0.458	0.601	31.2%	0.574	25.4%	0.543	18.7%	0.506	10.5%
Bottom 10 countries	Thailand	0.722	0.678	0.650	-4.1%	0.658	-3.1%	0.665	-2.0%	0.672	-1.0%
	Viet Nam	0.638	0.645	0.618	-4.2%	0.625	-3.1%	0.632	-2.0%	0.638	-1.0%
	Saint Lucia	0.714	0.739	0.706	-4.5%	0.714	-3.3%	0.723	-2.2%	0.731	-1.1%
	Republic of Korea	0.891	0.868	0.827	-4.7%	0.838	-3.4%	0.848	-2.2%	0.858	-1.1%
	Grenada	0.744	0.744	0.702	-5.7%	0.713	-4.2%	0.724	-2.7%	0.734	-1.3%
	Haiti	0.471	0.430	0.387	-9.9%	0.399	-7.1%	0.410	-4.6%	0.421	-2.2%
	Maldives	0.698	0.703	0.631	-10.3%	0.651	-7.4%	0.670	-4.7%	0.687	-2.3%
	Malta	0.829	0.726	0.605	-16.8%	0.642	-11.6%	0.674	-7.2%	0.702	-3.4%
	Bangladesh	0.558	0.508	0.375	-26.3%	0.421	-17.1%	0.456	-10.3%	0.484	-4.7%
	Hong Kong	0.891	0.870	0.606	-30.4%	0.703	-19.2%	0.771	-11.4%	0.825	-5.2%

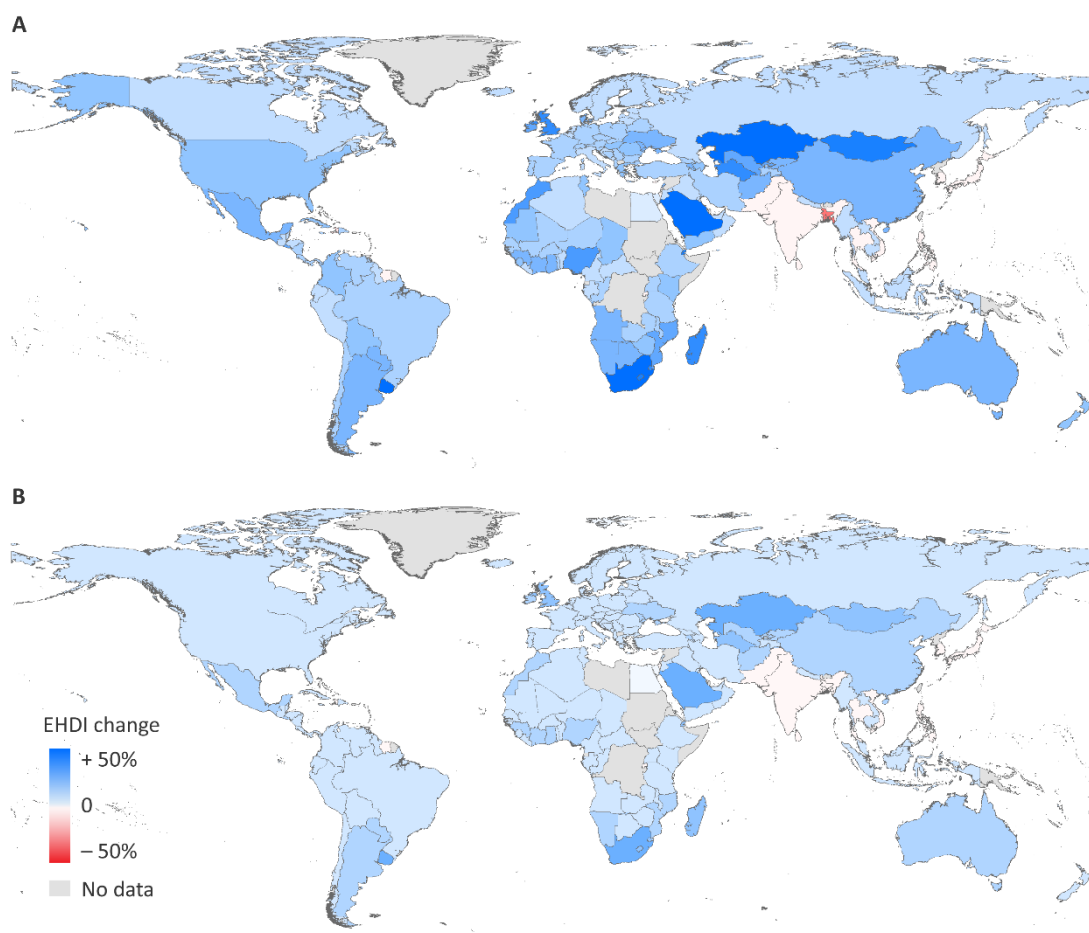


Figure 3. World maps showing the Environmentally-adjusted Human Development Index (EHDI) change caused by natural land cover index change under scenarios of 100% (A) and 25% (B) of substitution of animal protein by vegetal protein. Blue tones indicate countries that would gain natural land cover and consequently improve their EHDI. Red tones indicate countries that would lose natural land cover, which would decrease their EHDI. The darker the color, the greater the change relatively to 2013 EHDI. Note that the intensity of natural land cover loss never matches the intensity of natural land cover gain. See Table S7 for detailed values.

Discussion

In this study, we calculated the change in agricultural area under scenarios of 25%, 50%, 75%, and 100% of substitution of animal protein by vegetal protein considering the 173 countries for which all required data was available. Assuming a given decrease in agricultural area has the potential to increase, to the same extent, the natural land cover (NLC) through the restoration of abandoned agricultural land and, conversely, an increase in agricultural land area implies further conversion of natural habitats into croplands, we automatically estimated the NLC area change for each country under each scenario. The NLC area change was then accounted for in the Environmentally-adjusted Human Development Index (EHDI), which allowed us to assess the impact of each protein substitution scenario in the development of human societies via their effect on countries' NLC area change.

Globally, substituting animal protein by vegetal protein would have a remarkable positive environmental outcome, as it could release from agriculture up to 3.1 billion ha (Table 1), an area roughly equivalent to approximately four times the size of Australia, or 20% of the world's land area. Considering the ability of passive restoration alone to transform abandoned farmland back into natural environments (Batchelor *et al.*, 2015; Pereira & Navarro, 2015; Crouzeilles *et al.*, 2017), such global agricultural land reduction would provide an opportunity for the restoration of approximately 967 million ha of forests, 826 million ha of grassland, 666 million ha of shrub lands, 596 million ha of naturally sparse vegetated areas, 43 million ha of aquatic or regularly flooded vegetation, and 4 million ha of mangroves (Table 2). These values represent a remarkable

opportunity for large-scale rewilding, with enormous benefits for biodiversity conservation.

Our estimation of the global agricultural area in 2013 (4,392,555,484 ha) is smaller than the value reported by FAO for the same year (4,883,426,630 ha) (Table S5). Such difference is explained because this study considers only the 44 crops that represent more than 90% of global calories production. However, our estimation of the proportion of all crops' area allocated to produce livestock feed (34%) and the proportion of global agricultural area allocated to produce animal products (73%) are in accordance with previous reports (Steinfeld *et al.*, 2006; Cassidy *et al.*, 2013) (Table S5). As the areas allocated to produce animal products and plant products were the basis for calculating the protein replace area and consequently the agricultural and NLC area changes, we are quite confident about our results.

At country level, a shift towards more plant-based diets would have a positive outcome for most countries. However, for 31 (18%) of the countries considered in the analysis, it would be accompanied by an increase of agricultural area. It is worth noting that 28 of those 31 countries are archipelagos and/or Asian countries (Table S3), the only exceptions being Israel, Rwanda, and Suriname. As suggested by the ratio between the proportion of fish in all protein and the proportion of non-fish animal products in all protein, agricultural area increase after protein substitution may be due to the high consumption of wild caught fish by these countries' inhabitants (Table S3). Furthermore, the absence of true values of permanent meadows and pastures (PMP) for Bermuda, Hong Kong, Japan, Malta, and Taiwan is at least partly behind the negative outcomes for these countries. As grasslands and shrub-covered areas are known to be largely

used as pastures, the PMP area for these countries are probably lower than the actual values, and thus most likely resulted in underestimated values of the area that would be spared in these countries after protein substitution. Another reason that might explain some increases in agricultural area is our decision to adjust the value of protein per capita per day for those countries below 63 g/capita/day. This is especially true for countries with low values of actual grand total protein per capita per day and/or highly populous, such as Bangladesh, Haiti, India, Philippines, Rwanda, and Thailand. In these cases, we argue an increase in agricultural area was inevitable, for eradicating malnutrition is as important as guaranteeing the preservation of nature. Pakistan and Israel are the only countries that are not in any of the situations just presented (Table S3). Moreover, it is remarkable that, for most countries with high fish consumption and/or adjusted protein per capita per day, the proposed dietary shift still reduces the current required agricultural area (Table S3), confirming the effectiveness of the substitution of animal protein by vegetal protein as a strategy to reduce our impact on natural environments.

It might also be worth noting that our study follows a conservative approach in another aspect. Because the total vegetal protein supply quantity refers to the 44 crops included in the analysis only, we possibly replaced some vegetal protein provided by sources such as aquatic plants and other plant products non-dependent on agricultural area, which might represent a significant proportion of grand total protein supply quantity in some countries.

Even if the arguments just presented are disregarded, not only the number of countries that benefit from protein substitution is much higher, but the total spared area in these countries is two orders of magnitude larger than the total

lost area in countries for which agricultural area increases after the same substitution (Table 1 and 2). Moreover, the mean gained area in relation to country area in the countries that gain area is more than the double of the mean lost area in the countries that lose area (Tables 1 and 2). It is also worth highlighting that these results inform about the potential of plant-based diets to spare not only terrestrial habitats, but also freshwater and marine ones. In those countries where additional agricultural area would be needed after the proposed dietary transition, benefits to aquatic animals and their habitats should be considered when deciding whether the transition would pay off.

An increase of agricultural area is undesirable from the perspective of nature conservation, especially in priority areas for conservation. However, we shall remember that the calories that are free to humans in terms of crop use are not necessarily free in terms of other direct and indirect impacts on biodiversity, such as depletion of commercial fish species, accidental mortality of non-target species in fishing gear, and habitat destruction caused by trawling and blast fishing (Pauly *et al.*, 1998; Lewinson *et al.*, 2014; Pauly *et al.*, 2016; Chapter 1 of this thesis). Moreover, the proposed dietary transition would also be immensely beneficial to the recovery of freshwater and coastal ecosystems (i.e., estuaries, sea-grass fields, shallow seas of continental shelves, coral reefs, mangroves, and tidal marshes), as well as to the species that depend on them. Such positive effects are expected because of the major role of the livestock sector as a driver of water pollution, which has undoubtedly contributed to put these habitats at great peril (Islam & Tanaka, 2004; Camargo & Alonso, 2006; Diaz & Rosenberg, 2008). Interestingly, these ecosystems are by far those with the highest monetary value of ecosystem services per unit of area (Costanza *et al.*, 1997; de Groot *et*

al., 2012; Costanza *et al.*, 2014), and thus their recovery also has a great potential to improve human well-being. Having this in mind, we argue the substitution of animal products by plant-based foods might still be recommended in countries for which our analysis predicted an increase of required agricultural area. In these cases, changing current international market patterns might help transferring unavoidable agricultural area increase to countries that benefit from the dietary transition and are considered less priority conservation regions.

In addition to creating extraordinary nature conservation opportunities, substituting animal protein by vegetal protein would also be highly beneficial for the development of human societies. The area required to agriculture under the proposed dietary change would decrease in the majority of the countries, allowing the restoration of natural land cover and consequent increase of the Environmentally-adjusted Human Development Index (EHDI) (Figure 3). Considering the mean of all the 167 countries for which the EHDI was calculated, the difference between the EHDI under the 100% substitution scenario (0.703) (Table 3) and the 2013 EHDI (0.656) (Table 3) was 0.047, meaning the complete substitution of animal protein by vegetal protein would increase the EHDI of the world's countries on average by 7% (Table 3). These values for the 25% substitution scenario were 0.015 points and 2% increase in relation to the 2013 EHDI. Such improvement, which is solely caused by the increase of the NLC index (the environmental dimension of the EHDI), is much higher than the world's HDI annual improvement in the last years. Despite being the result of the efforts to increase the health, education, and income dimensions of human development, from 2014 to 2017, the world's HDI has increased no more than 0.004 points, corresponding to about 0.6% on average among consecutive years

(Table S8). Although a complete substitution of animal protein by vegetal protein is not a realistic goal in the short term (in fact, it may never occur), the comparison just presented suggests public policies promoting the proposed dietary transition constitute a valuable strategy to accomplish sound increases in human populations' development level. Moreover, it suggests such strategy is possibly more efficient than the ongoing efforts to increase the health, education, and income dimensions of human development.

We believe future studies investigating the effect of the proposed dietary transition on human development via its impact on the health dimension would further emphasize its benefits. Recent research has revealed that plant-based diets composed of vegetables, fruits, whole grains, and seeds can prevent, arrest, and even reverse common non-communicable diseases (Greger, 2016), which are currently the leading cause of death and responsible for 70% of all mortality worldwide (WHO, 2017). Thus, a shift towards more plant-based diets would probably lead to increased life expectancy (the health dimension of the Human Development Index). Additionally, it is also worth investigating the extent to which a global reduction in the consumption of animal products would improve human populations' health through better food security and fresh water availability.

It is important to acknowledge the cultural and behavioral obstacles to a shift towards plant-based diets. A food security-oriented strategy that might help the transition consists in establishing that feed production must not compete with food production (Cassidy *et al.*, 2013; Schader *et al.*, 2015). The implementation of greenhouse gases and water taxes on foods with heavy ecological impact has also been considered a valuable and even needed strategy to tackle the environmental burden of the present food system (Naylor *et al.*, 2005; Smith *et*

al., 2010; Hoekstra & Wiedmann, 2014; Wellesley *et al.*, 2015; Briggs *et al.*, 2016; Visconti *et al.*, 2016). In addition, eliminating subsidies to the livestock and fisheries sectors and providing adequate incentives to the supply chains of healthy foods would have an important role to play (Steinfeld *et al.*, 2006; Donati *et al.*, 2016). Finally, these approaches can be applied concomitantly with informed direct encouraging of the desirable dietary change, which can be especially efficient when specific consumer groups are targeted (Apostolidis & McLeay, 2016; de Boer & Aiking, 2017; Silva & Fischer, 2017). As the proposed dietary change would likely be accompanied by positive public health and food security outcomes in addition to environmental preservation (Tilman & Clark, 2014; Springmann *et al.*, 2016; Willett *et al.*, 2019), what seems to be a too radical recommendation might be transformed into a moral and culturally acceptable one.

Conclusion

Habitat availability is a key factor ultimately determining whether species thrive or go extinct. This study confirms the inefficiency of animal-based foods' production in terms of area requirements found in previous studies (e.g., Nijdam *et al.*, 2012; Alexander *et al.*, 2016; Davis *et al.*, 2016; Clark & Tilman, 2017), and shows the transition to more plant-based diets constitutes a valuable opportunity to the restoration of terrestrial habitats currently dedicated to feed livestock. Besides, this study shows the proposed dietary transition would greatly benefit aquatic ecosystems and their species. Although wild caught fish (which represent no burden to agricultural land) were included in the animal protein to replace, the substitution of animal protein by vegetal protein is nonetheless accompanied by

a decrease in agricultural area in the majority of the world's countries. This indicates the proposed dietary shift not only has a great potential to recover vast extensions of terrestrial habitats, but it also represents a remarkable prospect for the conservation of both commercial fish species and non-target aquatic animals that are threatened by bycatch and habitat destruction caused by fishing activities (Pauly *et al.*, 1998; Pauly *et al.*, 2002; Lewinson *et al.*, 2004; Lewinson *et al.*, 2014; Oliver *et al.*, 2015; Chapter 1 of this thesis).

This study also illustrates the enormous potential of a transition towards plant-based diets to improve human development through increased natural land cover, which we estimate to be as effective as achievements in the health, education, and income dimensions of our societies. Moreover, it is in accordance with the growing evidence that long-term human development and nature conservation might be interdependent rather than incompatible goals (e.g., Griggs *et al.*, 2013; Tilman & Clark, 2014; Westhoek *et al.*, 2014; Chapter 2 of this thesis).

For these reasons, we argue that a the dietary transition towards more plant-based diets is probably the most cost-effective single strategy to minimize the impact of human populations on the environment, while also contributing to the improvement of human development. Although this study's estimates are based on the assumption that the substitution of animal protein by plant protein happens in equal degree in all countries simultaneously, isolated initiatives would always be benefic and worth taking.

Notes

Note 1. The value for Egypt was actually the lowest, but since this is one of the countries for which FAO's database gives no value of PMP, we have decided to present the country with the nearest positive value.

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Supplementary Material

Available at:

<https://drive.google.com/open?id=1ps8BrVhK3ecNRNgHwqAhGrNmoPgMhi83>

Table S1. Food items used in the analysis, their correspondence between FAO's food balance sheet (FBS) and crops (QC) datasets, their protein content as calculated by dividing protein supply quantity by food supply quantity based on FBS data for the world, their protein content according to Young and Pellet (1994), and the difference between these values.

Table S2. Oil content for each oil crop considered in the analysis. The values were obtained from Weiss (2000) *apud* Cassidy *et al.* (2013).

Table S3. Grand total protein supply quantity, as well as protein supply quantity from animal products, fish and seafood, and non-fish animal products by country. The 39 countries with an actual value of grand total protein supply quantity <63 are indicated as "true" in the adjusted value column. The difference between adjusted and actual values is also presented. The proportions of fish and non-fish animal products in grand total, together with the ratio between them, indicate the weight of fish in replace protein. The ratio was used to rank the countries as presented. The 31 red-shaded countries are those for which substituting animal protein by vegetal protein produces an increase in agricultural area change. The seven countries with no value of permanent meadows and pastures (PMP) are indicated as "true" in the no value column. The adjusted value (produced by subtracting the agricultural area from the sum of herbaceous and woody crops)

is also presented. The * in Bermuda indicates the adjusted value was fixed in zero. All protein supply quantity values are given in g/capita/day. PMP adjusted values are given in ha.

Table S4. Results of the analysis performed to estimate the agricultural area change (AAC) that would occur in 173 countries under four scenarios of substitution of animal protein by vegetal protein. The relative agricultural area change (RAAC – the proportion of AAC in relation to respective country area) is also indicated. The first six rows are a summary of the results. The area allocated to produce replacing protein refers to the 100% substitution scenario. Absolute areas are given in ha and are rounded to the nearest integer. Countries are sorted by RAAC. AP = animal products; PMP = permanent meadows and pastures; PP = plant products. Countries where agricultural area decreases and increases are indicated with blue and red shades, respectively.

Table S5. Estimated global agricultural area (EGGA) and its allocation considering the 173 countries and the 44 crops included in the analyses. Global agricultural area (GAA) according to Food and Agriculture Organizations' (FAO) Land Use domain is also given, as well as the proportion of each area in relation to all crops area, EGGA, and GGA. All values refer to the year 2013. Areas are given in ha. All values are rounded to the nearest integer.

Table S6. The natural land cover area change (NLCAC) and the relative natural land cover area change (RNLCAC – the proportion of NLCAC in relation to respective country area) under four scenarios of substitution of animal protein by

vegetal protein for the 173 countries included in the analysis. Absolute and relative distribution of NLCAC among the following six natural land cover (NLC) categories are also given: tree-covered areas (Tree), shrub-covered areas (Shrb), grassland (Gras), sparsely natural vegetated areas (Spar), aquatic or regularly flooded areas (Floo), and mangroves (Mang). This distribution follows the relative proportion of the NLC categories in each country as in 2013. The first six rows are a summary of the results. Absolute areas are given in ha and are rounded to the nearest integer. The RNLCAC was used to rank the countries. Countries where NLC area increases and decreases are indicated with blue and red shades, respectively.

Table S7. Environmentally-adjusted Human Development Index (EHDI) values for 167 countries under four scenarios of substitution of animal protein by vegetal protein, as well as their respective proportional change in relation to the EHDI as in 2013. These estimations are based on the natural land cover area change produced by such substitution (see Table S6), and considering the Human Development Index (HDI) as in 2013. The first three rows are a summary of the results. Countries where the EHDI increases and decreases are indicated with blue and red shades, respectively.

Table S8. The World's Human Development Index (HDI) for four consecutive years. Data obtained from the United Nation's 2018 Statistical Update of the Human Development Indices and Indicators report (United Nations, 2018). The absolute difference and the proportional change in relation to the previous year are also given.

Script S1. Analysis code used to calculate the area allocated to produce animal and plant products, the area needed to replace animal protein by vegetal protein, and the agricultural area change by country under scenarios of 25%, 50%, 75% and 100% of substitution of animal protein by vegetal protein.

Supplementary Material's References

Cassidy, E.S., West, P.C., Gerber, J.S. & Foley, J.A. 2013. Redefining agricultural yields: from tonnes to people nourished per hectare. Environ. Res. Lett. 8: 034015.

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CONCLUSIONS AND PERSPECTIVES

This thesis presents novel foundations for the pertinence of linking food choices with global nature conservation and human well-being aspirations. Although the opinion that human carnivory is a leading player on the ongoing biodiversity crisis is gaining momentum, no studies to date have been designed to comprehensively assess its global impact. After systematically reviewing the several mechanisms by which human carnivory threatens biodiversity and separating them from the impacts of general agriculture, this thesis' first chapter conservatively estimates that, among other major aspects of human ecology, human carnivory can be considered the major single driver of species decline and extinction. By showing that natural land cover and overall life satisfaction are positively correlated at country level, the second chapter not only supports the idea that nature conservation and long-term development goals are interdependent, but also that livestock's inefficiency in terms of agricultural land requirement is an obstacle to human development.

As a solution to the problems discussed in the first and second chapters, the third chapter highlights the exceptional potential of the proposed dietary shift to create wide-ranging opportunities to both nature conservation and human development. This chapter shows that, after considering the additional cropland that would be required to replace 25%, 50%, 75%, and 100% of animal protein consumed by humans by vegetal protein, one to four times the area of Australia would be globally freed from agriculture. Such vast tracts of land left to passive restoration alone would create an extraordinary opportunity to bring biodiversity and ecosystem services back. Remarkably, protein quantity from wild caught fish

is also included in the total animal protein, meaning the proposed dietary transition also constitutes a solution to the overexploitation of marine and freshwater species.

We live in a time of reckless destruction of the last of the wild, with dire consequences to other species and generations to come. Curiously, more than ever, humans acknowledge the ecological principles operating on the planet with fair accuracy, and are able to identify solutions to the environmental problems that threaten their future. Therefore, lack of understanding can no longer be evoked as a justification to inaction. As facultative consumption patterns are the strongest determiners of huge environmental impacts such as those caused by human animalivory, it is time to seriously consider investing in strategies to change human behavior as the solution to these perils. Doing so is probably the most effective way to close the research-implementation gap that currently hampers effective nature conservation and human development.

The proposed dietary transition is especially advisable and even morally grounded because, in addition to the much desirable environmental outcomes it produces, there is so much to gain in numerous dimensions of the human condition. Hopefully, such happy arrangement might be used to change global perceptions concerning acceptable consumption patterns when producing the much needed material intended to general public education and awareness. Taxation of environmental and health externalities of animal-based foods' production and consumption, besides the withdrawal of fisheries and livestock subsidies, are some of the options to counteract the purely economically-driven obstacles to the proposed dietary transition.

For the worst and for the better, true nature conservation is ultimately about changing human behavior. While this surely is not an easy task, it is one that depends solely on ourselves. While promoting a global shift towards diets majorly based on plants might be dismissed as too drastic or radical, it is probably our best opportunity to reconcile nature preservation with long-term human development. If we fail to implement solutions with immense benefits and virtually no drawbacks in useful time, then there is no reason to believe we can do much else. While our strenuous conservation efforts might win some battles, they will have just postponed the inevitable catastrophic ending of the war for biodiversity conservation and true human prosperity.