

Averting wildlife-borne infectious disease epidemics requires a focus on socio-ecological drivers and a redesign of the global food system

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Summary

A debate has emerged over the potential socio-ecological drivers of wildlife-origin zoonotic disease outbreaks and emerging infectious disease (EID) events. This Review explores the extent to which the incidence of wildlife-origin infectious disease outbreaks, which are likely to include devastating pandemics like HIV/AIDS and COVID-19, may be linked to excessive and increasing rates of tropical deforestation for agricultural food production and wild meat hunting and trade, which are further related to contemporary ecological crises such as global warming and mass species extinction. Here we explore a set of precautionary responses to wildlife-origin zoonosis threat, including: a) limiting human encroachment into tropical wildlands by promoting a global transition to diets low in livestock source foods; b) containing tropical wild meat hunting and trade by curbing urban wild meat demand, while securing access for indigenous people and local communities in remote subsistence areas; and c) improving biosecurity and other strategies to break zoonosis transmission pathways at the wildlife-human interface and along animal source food supply chains.

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Introduction – trends and causes of wildlife-origin infectious diseases

Zoonoses are infectious diseases caused by pathogens (bacterial, viral or parasitic) transmitted from vertebrate animals (wild or domesticated) to humans, including those transmitted through an arthropod vector¹ (Figure 1). Such diseases are classified as emerging infectious diseases (EIDs) when they have recently entered the human population for the first time, or

when they have been present in humans historically but have recently increased in incidence or geographic range, or have re-emerged as a new variant^{2,3} (see Webappendix 1. Glossary of human infectious disease-related terms). Zoonotic disease outbreaks and EIDs can pose a significant threat to public health and global economies,^{4,5} and their frequency,^{2,3,6–8} capacity to geographically spread⁹ and economic impacts^{10,11} have been asserted to be on the rise.

Throughout human history, major alterations in the human disease burden have largely resulted from anthropogenic (i.e. demographic and socio-economic)

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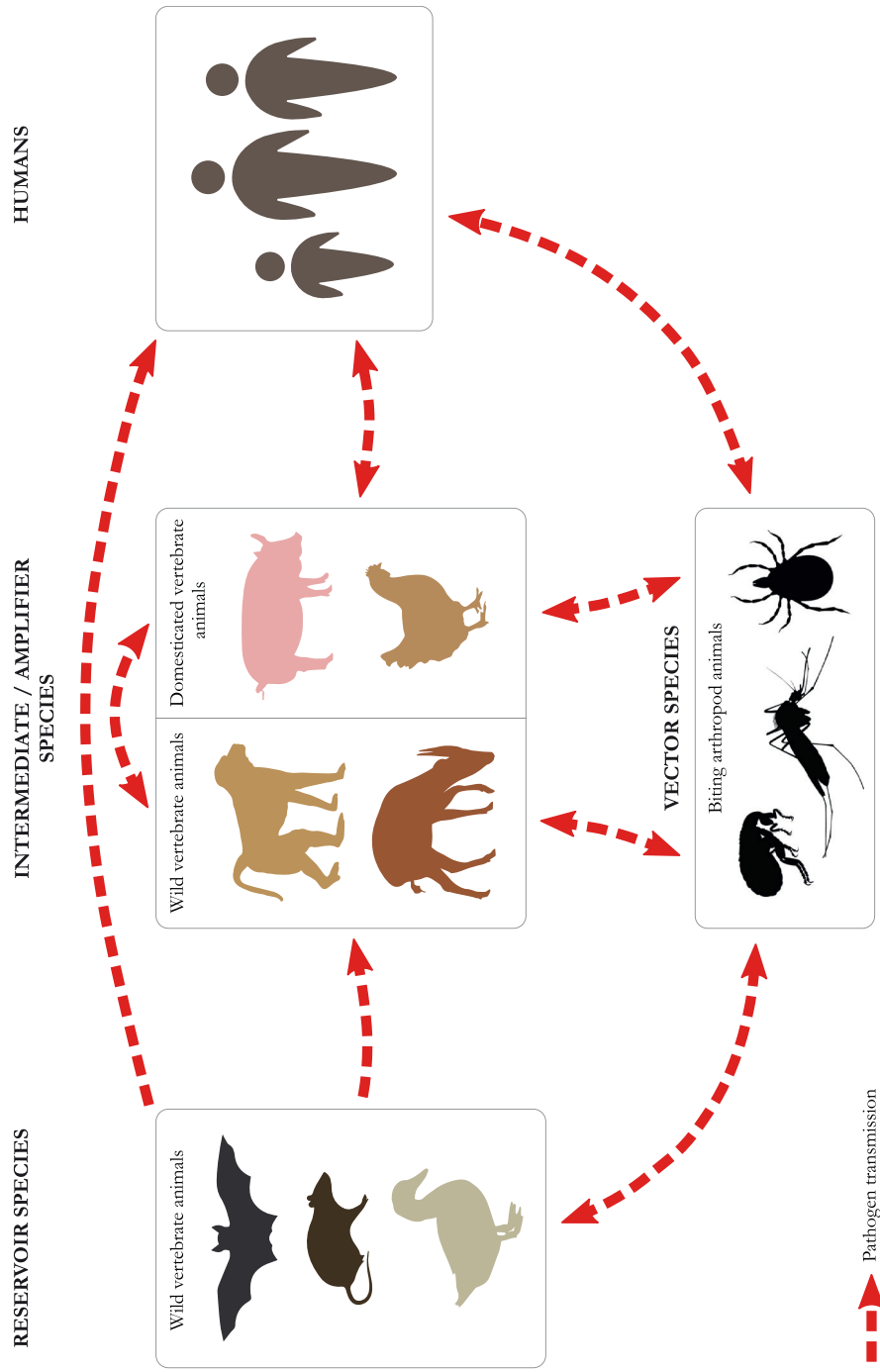


Figure 1. Zoonosis transmission pathways.

changes. The emergence of many of today's better known human contagious diseases was associated with the Neolithic revolution of 12,000 years ago, when small hunter-gatherer groups settled into agricultural villages to cultivate crops and raise domesticated animals, and later congregated in larger towns and cities.^{12,13} Several human-specific pathogens such as smallpox, measles, mumps and tuberculosis are believed to have originated from the domestication of mammalian and avian animals during this period.^{14–16} Although some other human-specific pathogens originated in wildlife much earlier, such as malaria's parasite (*Plasmodium falciparum*), which is likely to have its origins in western gorillas (*Gorilla gorilla*).¹⁷ Over time, the increase in incidence and spread of diseases have been facilitated by human and livestock population growth, urbanisation, travel, trade, wars, the colonisation of territories and globalisation^{13,18–20} (see Webappendix 2. *Human movement and infectious diseases*). The Human Immunodeficiency Virus (HIV/AIDS) pandemic provides an illustration of some of these co-occurring processes (see Webappendix 3. *The socio-economic origins of the HIV/AIDS pandemic*).

Beginning in the second half of the 19th century, the infectious disease burden in human societies has been progressively reduced through public sanitation, improved nutrition, widespread childhood vaccination and the introduction of antimicrobials. Outbreak cases per capita (i.e. the total number of people infected as a proportion of a nation's population in an outbreak year) also appear to have been declining over time, thanks to global improvements in prevention, early detection, control and treatment.³ In the US, for example, in 1850 all 10 leading causes of death were infectious diseases (tuberculosis, cholera, malaria, etc.); by 2010, the 10 leading causes of death were non-communicable diseases (cancer, stroke, Alzheimer's disease, etc.), except for influenza/pneumonia.²¹ Non-communicable diseases such as diabetes and ischaemic heart disease are now the leading causes of premature mortality²² and disability²³ in most regions of the globe.

Nevertheless, some analyses suggest that over the past half century or so the risk of zoonotic disease emergence (as measured by the number of first-occurrence zoonotic EID 'events'² and the frequency and richness of zoonotic disease outbreaks³) and subsequent epidemics and pandemics^{8,13} has been increasing. More specifically, Jones and colleagues² observe an increasing incidence of zoonotic EID events between 1940–2004, with more than 70% of these events being caused by pathogens with a wildlife origin, such as Ebola virus, Nipah virus and SARS coronavirus (SARS-CoV). Smith and colleagues³ identify a rise in the number and richness of zoonotic disease outbreaks between 1980–2013

(12,012 in total, affecting every country in the world), including among the causes pathogens such as anthrax, chikungunya and tuberculosis. Although the veracity of such trends is still open to conjecture (see Webappendix 4. *Limits of available zoonotic disease datasets and spatio-temporal trend analyses*), numerous proponents have argued that zoonoses, and especially those from wildlife, may have been emerging and re-emerging at an unprecedented and increasing rate in recent decades.^{2,3,6–8,24} For example, of the seven coronaviruses known to infect humans, three (those causing Severe Acute Respiratory Syndrome (SARS), Middle East respiratory syndrome (MERS) and Coronavirus Disease-19 (COVID-19)) have emerged within the past 18 years²⁵ (although it is difficult to assess trends from such small sample size). And of the 11 Ebola outbreaks that occurred in DRC since the 1970s, six took place in the past decade (some probably stemming from viral resurgence in survivors of previous outbreaks²⁶ in a context of rising human population density and mobility²⁷).

The ongoing occurrence and potentially increasing trend or increasing relative importance of wildlife-origin zoonotic outbreaks and EIDs are likely to represent a 'hidden cost' of socio-economic development and globalisation over the past century, being linked to faster human and livestock population growth, heightened urbanization and human crowding,¹³ accelerated encroachment into natural habitats and agricultural intensification,²⁸ increased antibiotic use resulting in multi-drug resistance²⁹ and the internationalisation of travel and trade.³⁰ As an example of the latter, while in 2002–3 it took over two months for SARS-CoV (the coronavirus causing SARS) to move from China to Hong Kong and then to the rest of the world, in 2019–20 SARS-CoV-2 (the coronavirus causing COVID-19) spread out of China much more rapidly. This was due to SARS-CoV-2's higher transmissibility³¹ and pre-symptomatic and asymptomatic infectiousness,³² but partly also to China's economic growth since 2003 and the related hastened expansion of domestic and international travel and trade.⁹

Some of the most important viral 'reservoirs' for infectious diseases of livestock and humans include bat, rodent and bird species that live in human-modified landscapes, and which are chronically or periodically infected with viruses that are either adapted to them, causing minimal or no disease, or that infect them asymptotically, but which may be pathogenic for humans^{33–35} (Figure 1). Among these are hantaviruses, arenaviruses, avian arboviruses and coronaviruses. For example, current evidence indicates that fruit bats (*Pteropus sp.*) are a reservoir host for henipaviruses like Nipah and Hendra,³⁶ that horseshoe bats (*Rhinolophus sp.*) are likely a natural host for betacoronaviruses like

SARS-CoV and SARS-CoV-2,^{37–39} and that fruit bats may act as a natural host for filoviruses like Marburg⁴⁰ and Ebola^{41,42} (although for some of these viruses the pathway of emergence and evolution from the ancestral strain to an epidemic human-to-human strain is not yet clear). Even though bats have been singled out as being particularly inclined to harbour zoonotic pathogens due to their flight-related immunological and ecological features,^{35,43} a recent study suggests that variation in the number of zoonoses among animal orders is simply a function of their species richness.⁴⁴

Many viruses make use of an ‘intermediate’ vertebrate host through which they can evolve and transit from the reservoir species to humans⁴⁵ (Figure 1). For instance, zoonotic spillover of Ebola has been associated by some analysts with the hunting, handling and consumption of meat from frugivorous animals (e.g. duiker antelopes, non-human primates) that may contract the virus by eating fruits partly consumed by infected bats.^{41,46} SARS-CoV is likely to have been transmitted from bats to wild animals such as the masked palm civet (*Paguma larvata*), and to have spilled from these into humans in live animal markets.^{37,47}

However, direct wildlife–human zoonosis transmission is relatively rarely documented,^{34,48} in part because these types of spillover events are difficult to detect and therefore likely to be under-reported, and in part because humans are more regularly in contact with domestic and peri-domestic animals than with wild animals. Instead, intensive livestock production and transportation systems are known to play a major role in increasing the likelihood of domesticated animals acting as intermediate and amplifier hosts^{34,49,50} for wildlife-origin diseases such as anthrax, Q fever, campylobacteriosis and many others (Figure 1). In the Nipah epidemic that broke out in Malaysia in the late 1990s, for instance, the virus – which spilled over from bats to pigs through fruit and pigsties contaminated with bat saliva and urine – quickly spread among pigs, and from pigs to humans, facilitated by high pig population and farm densities⁵¹.

Other zoonotic diseases are transmitted from wild animals to humans through biting arthropod vectors such as mosquitoes, ticks and fleas (Figure 1). For example, evidence suggests that the four known Dengue virus serotypes were originally transmitted from monkeys to humans through *Aedes* mosquitoes in tropical Africa and Asia, and that there is potential for the re-emergence of sylvatic dengue in the human transmission cycle as a result of deforestation, climate change and geographic expansion of its mosquito vector.⁵² In the Western Ghats region of southern India, the tick-borne viral Kyasanur Forest Disease, which is believed to have monkey species as amplifying hosts and cattle as nutrition hosts, has been expanding rapidly beyond

its endemic range over the past two decades, affecting an increasing number of low-income forest communities.⁵³

Some EIDs believed to have their origin in wildlife have resulted in regional outbreaks or global pandemics that have caused extensive mortality, exceptional economic losses and widening social inequalities. Since its first detection in 1981, HIV-1/M has caused more than 32 million deaths,⁵⁴ and to date the prospects of curative treatment or an effective vaccine remain uncertain.⁵⁵ In 2020, the COVID-19 pandemic caused more than 1.8 million deaths in a year⁵⁶ and resulted in the steepest global economic slowdown since the Great Depression of the 1930s,⁵⁷ with developing countries the least capable of withstanding the economic shockwave.⁵

In this Review, we explore the emerging debate over some of the key potential socio-ecological drivers of wildlife-origin zoonotic disease outbreaks and EID events. Although this scholarship is still in its infancy, being mostly model-based and lacking sufficient empirical corroboration, it is nonetheless worthwhile to investigate the extent to which the incidence of wildlife-borne zoonosis outbreaks, which are likely to include devastating pandemics like HIV/AIDS^{58–60} and COVID-19,^{61–63} may be linked to forms of ecosystem degradation such as tropical deforestation for agricultural food production and over-harvesting of wild animals for food consumption, and as such may be related to contemporary ecological crises such as global warming and mass species extinction (section 3). A second objective of the Review is to explore policy recommendations and social actions – such as a global transition to more plant-based diets and the curbing of tropical urban wild meat demand – which are increasingly deemed necessary to tackle climate change and biodiversity loss, and which, pending further research, may also prove beneficial for containing the risk of wildlife-borne infectious disease outbreaks and pandemics (sections 4–7). Biosecurity and other strategies to break zoonosis transmission pathways at the wildlife–human interface and along animal source food supply chains are also discussed (section 8).

Search strategy and selection criteria

In this Review we do not aim at providing a systematic literature review with quantitative synthesis of results, but rather a critical synthesis and detailed expert viewpoint of the issues related to wildlife-borne zoonotic disease risk and the global food system.

Information on zoonotic epidemic and pandemic risk, global livestock production systems and tropical wild meat hunting and trade was sourced by searches of Google Scholar and the reference lists of relevant peer-reviewed articles and books. Different combinations of

multiple search terms relevant to the analysis were used, such as “emerging infectious disease”, “zoonosis”, “epidemic”, “pandemic”, “cross-species transmissions”, “spillover”, “reservoir population”, “intermediate host”, “amplifier host”, “livestock”, “intensive farming”, “deforestation”, “forest encroachment”, “habitat fragmentation”, “forest edge”, “biodiversity dilution effect”, “wildlife”, “wild meat hunting”, “wild meat trade”, “global food system”, “plant-based diet”, “flexitarian diet”, “sustainable agriculture”, “sustainable intensification”, “organic farming”, “agroecology”, “livestock product taxation”, “wild meat ban”, “consumer campaign”, “community-based wildlife management”, “sustainable hunting”, “biosecurity” and “One Health”. Only articles and books published in English were included.

Socio-ecological drivers of wildlife-origin infectious diseases – tropical deforestation for livestock production and wild meat hunting and trade

Following the emergence of SARS-CoV-2 in China and its global spread resulting in the COVID-19 pandemic, a number of infectious disease and wildlife conservation scientists,^{11,64,65} as well as high-profile international bodies such as the World Health Organization (WHO), the World Organisation for Animal Health (OIE) and the United Nations Environment Programme (UNEP),⁶⁶ pointed to tropical wild meat hunting and trade as a key driver of this and other disease outbreaks.

While game hunting for by-products and sport is practiced all over the world, in the tropical and subtropical forest regions of Africa, Asia and South America, over the past 30 years hunting pressure to supply the growing wild meat demand of rapidly expanding rural and urban populations has radically increased.^{67–70} The progressive penetration of hunters into remote pristine forests, and their gradual depletion of local populations of game species, has caused significant wildlife population declines^{68,71} and sometimes led to a state of defaunation in which the trees are preserved but larger-bodied mammals are absent.^{67,69,70} A decline in larger-bodied frugivores is also predicted to undermine seedling recruitment for bigger-seeded, heavy-wooded, long-lived tree species, which could reduce the carbon storage capacity of tropical forests.⁷² In addition to these ecological threats, it is argued, the hunting, transport, marketing, butchering and consumption of wild meat can also facilitate the emergence of zoonoses and so involve serious public health hazards.^{11,64,65,73}

Other analysts have rebutted that the wild meat infection risk remains poorly understood, requiring cautious judgement about its role in zoonosis emergence,^{50,74,75}

and that on a global scale such risk is likely to be significantly lower than that posed by intensive livestock production systems where high population density, low genetic diversity and immunosuppression enable rapid pathogen spread and mutation.^{28,50,76} For example, the 2009 swine influenza pandemic, which was caused by an A/H1N1 reassortant virus with gene segments from birds, North American pigs, Eurasian pigs and humans, is most likely to have originated in industrial pig farms in Mexico.⁷⁷

However, although the infection risk from wild meat hunting and handling along the supply chain is unquantified and may be small, human diseases have nonetheless emerged and re-emerged from these practices, sometimes causing immense health and socio-economic damage. Such spillover events are likely to include some of the deadliest epidemic viral diseases, such as HIV^{59,78} and Ebola virus in Central and West Africa,^{41,42,46} Hepatitis E virus in Japan⁷⁹ and SARS coronavirus in China.^{37,47} This, it is argued, justifies subscribing to the precautionary principle in developing wild meat policies aimed at containing the risk of infection. Whether a wild meat-related zoonotic pathogen is entirely transmitted to humans by spillover (e.g. rabies,⁸⁰ toxoplasmosis⁸¹) or whether it may be transmitted by a combination of spillover and human-to-human epidemic dynamics (e.g. Lassa virus,⁸² Ebola virus,²⁶ SARS-CoV-2⁸³), prevention of one rare spillover event could avert tens, hundreds or thousands of downstream human cases.^{11,84}

It has been partly on the basis of such precautionary principle that blanket bans on wild meat have been invoked by some animal welfare and wildlife conservation groups^{85–88} and implemented by some governments.^{89,90} Yet, policy interventions must be critically assessed in the broader context of related pros and cons to avoid counterproductive outcomes. Blanket bans tend to be ineffective in reducing wild meat hunting and trade in tropical regions,^{91–96} and could have detrimental impacts on both Indigenous Peoples and Local Communities (IPLCs)^{97–100} and wildlife conservation.^{101,102} Importantly, these bans also risk being counterproductive in reducing the threat of emergence and spread of wildlife-borne diseases, for two reasons: first, they may force trade underground where it is harder to enforce biosecurity measures, and second, they may detract attention from other critical intervention points such as the causes of human-to-human contagion.^{89,103}

Other scientists have focused on broader ecosystemic dynamics, identifying natural habitat destruction as a potential key driver of wildlife-origin infectious disease outbreaks. Human-mediated changes to natural ecosystems can increase the risk of zoonotic spillover by altering reservoir host density, distribution and susceptibility; pathogen prevalence, survival and dissemination; and reservoir host–human contact rates.¹⁰⁴ For example, tropical

deforestation has been observed to disrupt local environmental conditions in ways that favour larval development and increase adult survivorship of mosquito vectors, and to cause a reduction in the abundance of animal species that prey on larvae and adults, so leading to an increased incidence of human malaria.¹⁰⁵

Given the ubiquity of viral biodiversity, the geographic pervasiveness of intensive farming and the globalisation of travel and trade, a pandemic can conceivably originate on any part of the planet inhabited by people.⁷⁴ Yet, it has been argued on the basis of some spatial models that the risk of zoonotic disease emergence (and, by extension, zoonotic-origin pandemics) may be more elevated in tropical areas undergoing high rates of deforestation.^{76,106–110} While there is need for cautious interpretation of results from these models (see Webappendix 4. *Limits of available zoonotic disease datasets and spatio-temporal trend analyses*), the potential implications of a correlation between an increase in wildlife-origin disease outbreaks and accelerated tropical deforestation are worth exploring.

The line of reasoning behind such a correlation is that higher wild mammal species diversity in tropical forests may increase the ‘depth’ of the pathogen pool from which novel infectious diseases emerge. Deforestation then creates transition areas (or ‘ecotones’) where the remnants of this biodiversity come into closer proximity with humans and livestock, generating new opportunities for inter-species pathogen transmission,^{28,111–113} and where the sylvatic pathogens they harbour are no longer controlled by environmental stochasticity.¹⁰⁹ The risk of zoonotic virus transmission has in fact been observed to be highest from domesticated mammals and wild rodent, bat, bird and primate species that have globally increased in abundance and/or expanded in range by adapting to human-dominated landscapes^{33,34} (Figure 2). Habitat fragmentation also increases the length of forest edges, which may increase the contact rate of humans and livestock with wildlife^{114,115} (although this is yet to be empirically validated).

For example, in Argentina, the emergence of Junin arenavirus (the causative agent of Argentine haemorrhagic fever) in the ‘humid pampa’ region has been linked to agricultural conversion and fragmentation of the prairie, which, by reducing the number of medium-size predators, may have enabled an upsurge in the virus’ reservoir host, the drylands vesper mouse (*Calomys musculus*).¹¹⁶ On the east coast of Australia, fruit bats’ forest habitat has been degraded on a large scale, increasing their dependency on flowering and fruiting trees planted in suburban or urban gardens, and so raising opportunities for Hendra virus spillover in domestic horses and humans.^{36,117}

There are also indications that habitat destruction and fragmentation and over-harvesting of wild animals

worsen the incidence of certain wildlife-borne human diseases by reducing vertebrate biodiversity in ways that increase the prevalence and abundance of animal species known to host zoonotic and vector-borne viruses.^{118,119} For instance, in parts of Africa, a significant decrease in the number of predators and large herbivore competitors is predicted to result in an increase in the number of rodent reservoir species.¹²⁰ In other words, habitat destruction and overhunting undermine biodiversity’s capacity to ‘dilute’ pathogen spread.¹²¹ Moreover, habitat degradation induces environmental stressors, such as crowding and food deprivation, which may increase wildlife susceptibility to pathogen infection and shedding.^{119,122}

Livestock production is the largest driver of natural habitat loss. About 40% of ice-free terrestrial surface is used for agricultural food production.^{123,124} Of this, around 75–80% is used as grazing land and cropland dedicated to cereal and soy feedstock production,^{123,125} and land dedicated to the cultivation of feedstock constitutes more than one third of total cropland,^{123,126} with about one third of global cereal production being fed to animals.¹²⁷ Although since the 1950s overall rates of natural habitat conversion to agriculture have slowed (the net area used for food production remaining constant since then),^{128,129} agricultural frontiers have gradually shifted from the temperate regions of Europe, North America and Russia to the tropical regions of Latin America, Southeast Asia and Africa, where rates of conversion of tropical forests and savannahs to agriculture are high,^{128,130} and where agricultural use of the land is less efficient.¹³¹ In South America, for example, between 1990–2005 about 71% of rainforest conversion has been for cattle grazing and around 14% for commercial cropping including soya for animal feed.¹³²

Grazing land and feedstock cultivation are therefore expanding into landscapes that host a significant share of the planet’s remaining natural habitats and are particularly rich in biodiversity¹³³ and carbon stocks.¹³⁴ As such, there are concerns that in addition to being responsible for the majority of agricultural food-related greenhouse gas (GHG) emissions^{134–137} and a prime driver of the current human-caused sixth mass extinction of species,^{138–140} livestock production may also increment the risk of wildlife-origin disease outbreaks by bringing humans and domestic animals into increasing contact with wild animal populations^{28,76,106,107,111,114} (Figure 2).

Although the pace of global population growth is slowing, the world population is projected to grow to around 9.7 billion people in 2050, and the most likely scenario is that it will continue growing throughout the present century.¹⁴¹ Despite large and growing inequalities (over 820 million people face chronic food deprivation and more than 2 billion people are micronutrient-deficient while 2.1 billion adults are overweight or obese),¹⁴² rapid economic growth in the

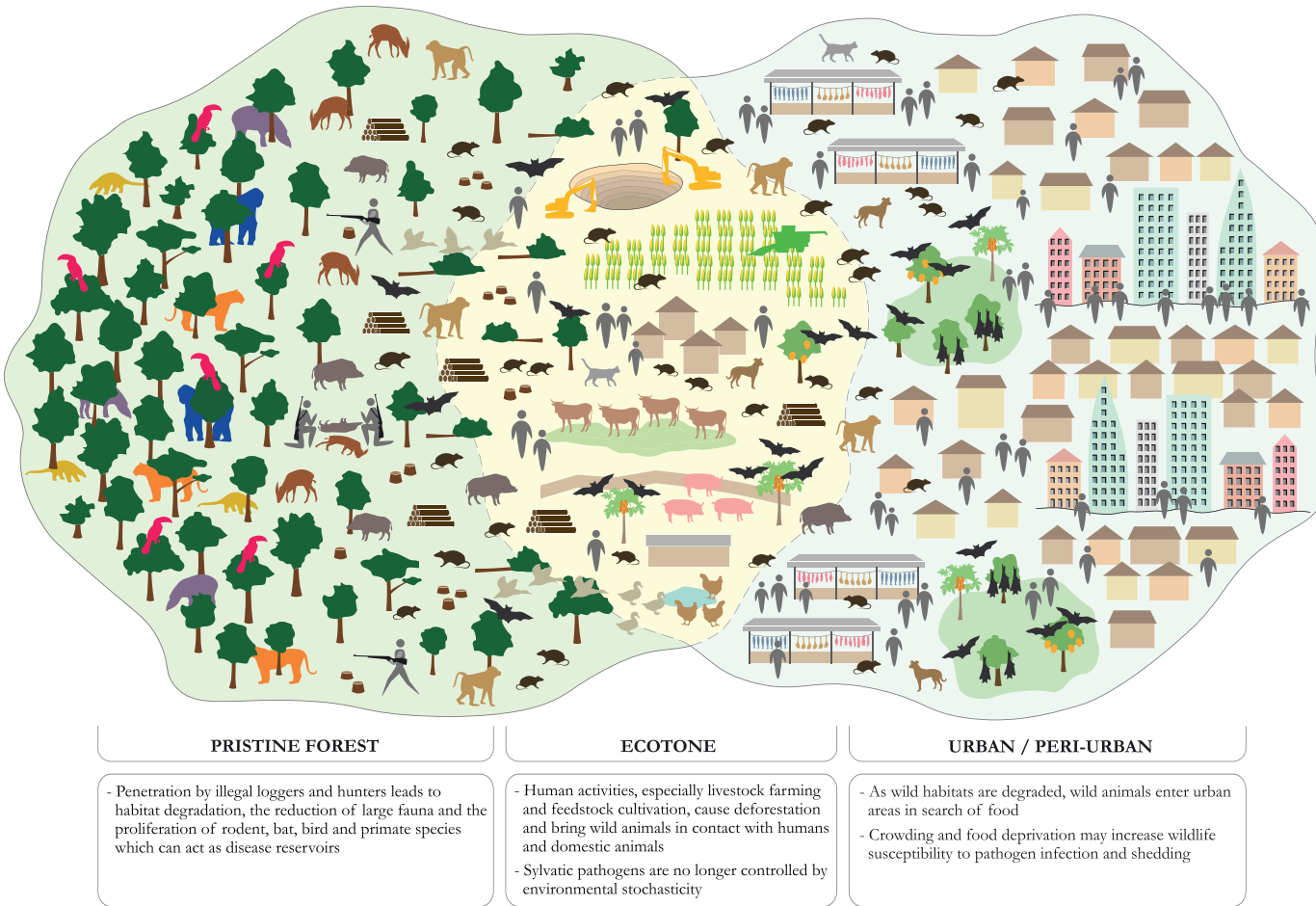


Figure 2. Tropical deforestation and overhunting as drivers of wildlife-origin zoonotic disease transmission

world's most populous developing countries means that, on average, the global population is predicted to become more affluent.¹⁴³ In advanced economies, per capita meat and dairy consumption has reached a plateau at environmentally unsustainable levels^{144,145} that often exceed health-based recommendations¹⁴⁶ (see Webappendix 5. *The human health, agronomic and food security benefits of predominantly plant-based (flexitarian) diets*). For example, the total area of agricultural land used within the UK and abroad to rear lamb, beef and dairy cattle for consumption within the UK has been calculated to be larger than the entire landmass of Great Britain.¹²⁹ A substantial increase in per capita meat and dairy consumption is also predicted in middle- and low-income countries^{147,148} (see Webappendix 6. *Animal source food consumption levels across different socio-economic and ecological contexts*). Furthermore, production of the amount of livestock meat that would be needed to replace urban wild meat consumption in the tropics would result in new large-scale land conversion.^{95,149} In the Congo Basin, for instance, replacement of an estimated wild meat yearly extraction of 4.5 million tonnes with local beef production would require the conversion of 25 million hectares of forest to pastures.¹⁵⁰

These trends imply that, in the absence of targeted mitigation measures, there is a strong risk that increasing global livestock production will greatly destabilise the planetary ecosystem processes on which the web of life and human wellbeing depend.^{136,151} Climate change is already causing global crop production losses¹⁵² and affecting food security in many regions¹⁵³ through increasing temperatures, changing precipitation patterns and greater frequency of some extreme events.¹³⁷ Climate change phenomena have also been implicated in the expansion of disease vectors' geographic ranges (e.g. summer temperature anomalies associated with outbreaks of West Nile Fever in South-east Europe)¹⁵⁴ and in the higher incidence of waterborne infectious diseases (e.g. rising sea surface temperature correlated with enhanced worldwide prevalence of *Vibrio* bacteria such as *V. cholera*).¹⁵⁵ If current population growth and dietary trends continue, GHG emissions from agricultural food production are likely to increase by about 30–40% by 2050,¹³⁷ and the target of keeping global warming well below 2°C is unlikely to be met.^{136,137,156,157} Meanwhile, the rate of species extinction is at present 100–1000 times the historical average,¹⁵⁸ with average species abundance likely to have fallen below the proposed 90% precautionary threshold.^{139,151} The negative impact of biodiversity loss on agricultural productivity alone has been estimated to warrant a moratorium on further land conversion.¹⁵⁹ There are concerns from some quarters of the scientific community that zoonotic diseases of wildlife origin may soon join global warming and wild species

extinction to constitute a third planetary ecological crisis.^{8,10,13}

There is, as we have repeatedly emphasised, an urgent need for empirical research to clarify the trends in the risk of wildlife-origin zoonotic disease outbreaks and EID events, and the potential geographical link of such risk with contemporary high rates of deforestation and wild meat hunting and trade in the tropics^{75,160} (see Webappendix 4. *Limits of available zoonotic disease datasets and spatio-temporal trend analyses*). Nonetheless, based on the above considerations, a set of precautionary responses to the wildlife-origin zoonotic disease threat can be delineated. Such responses include: a) limiting human encroachment into remaining tropical wildlands by promoting a global transition to diets low in livestock source foods; b) containing tropical wild meat hunting and trade by curbing tropical urban wild meat demand while securing IPLC's access through community-based wild game management; and c) improving biosecurity measures along animal source food supply chains, from hunting grounds and livestock and wildlife farms to rural and urban abattoirs and markets, and exploring other measures to break zoonosis transmission pathways at the wildlife–human interface. The remainder of this Review discusses each of this set of strategies.

Preventing natural habitat encroachment by combining sustainable agriculture and a global reduction of livestock source food production

Agricultural food production is one of the greatest sources of environmental degradation,^{125,128} and the global food system is responsible for up to one-third of all GHG emissions.¹⁶¹ Livestock production in particular has the highest environmental footprint (impact per unit product) of all foods in terms of land and water use, GHG emissions and eutrophication and acidification of aquatic and terrestrial systems.^{123,135,156,162–164} This is especially true for GHG emissions^{134,136} and pollutants that result in the formation of fine particulate matter (PM_{2.5}).¹⁶⁵ Due to livestock's low 'feed to meat' conversion ratios, manure-related emissions and ruminants' enteric fermentation,^{126,135} livestock source foods are responsible for about 75% of total agricultural food-related methane and nitrous oxide emissions,¹³⁶ and for about 15% of all anthropogenic GHG emissions, including carbon dioxide.¹³⁴ PM_{2.5} poses a severe threat to human health,¹⁶⁵ and is potentially also associated with COVID-19 morbidity and mortality rates.¹⁶⁶

Crucially, expansion of grazing land and feedstock cultivation in tropical forests, grasslands and

wetlands rich in biodiversity and carbon stocks is responsible for major biodiversity losses^{133,140} and GHG release into the atmosphere,^{134,137} as well as for the creation of ecotones that have been hypothesised to increase the risk of wildlife-borne infectious disease outbreaks.^{28,106,107,111,114} As seen in the previous section, not only does natural habitat clearing for livestock agriculture precipitate closer proximity of wildlife with humans and domestic animals.^{28,76,111,113} It also effects non-random patterns of defaunation, causing the loss of large- and medium-bodied herbivores and predators while favouring populations of rodent, bat, bird and primate species that are common zoonotic pathogen reservoirs^{33,34,119,121} (Figure 2).

This section therefore discusses the necessity of a global shift to predominantly plant-based diets in order to reduce the consumption and production of livestock source foods for environmental and public health purposes. It considers this strategy in relation to some of the main current approaches to sustainable agricultural production, namely sustainable intensification, organic farming and industrial-engineering initiatives such as soil-less vertical farming. The following section then explores the range of measures currently available to governments, civil society and the private sector to promote a reduction in the global consumption of livestock source foods.

In the past two decades, the global capacity to continue increasing the food supply appears to have been declining,¹⁶⁷ as highlighted by slowing rates of yield increase for the world's major staple grains (maize, wheat, rice, soy), the increasing role of cropland expansion in their production growth, and recent episodes of abrupt spikes in their prices.¹⁶⁸ These alarm bells urged a call for a sustainable intensification of global agriculture capable of increasing yields at the aggregate level (and so prevent further agricultural 'extensification' onto natural habitats) while also curbing environmental impacts per unit product. The use of the term 'sustainable intensification' has generated some controversy,¹⁶⁹ but its core intention is to highlight that satisfactory agricultural yields are possible without detrimental environmental impacts, if the current agricultural system responsible for wasteful resource use and chemical pollution is improved through better application of management practices and technologies.¹⁷⁰

However, although management practices and technologies exist that would enable improvements in agricultural yields with less environmental impact (e.g. drought- and pest-resistant cultivars, diversified cropping, minimum or zero tillage, improved slurry application, precision farming, enhanced livestock breeding, methane-reducing cattle feed additives, agroforestry, silvopasture, better water storage),^{171–173} their

cost-effectiveness and level of adoption are uncertain and highly reliant on investment in public infrastructure, farmer incentive schemes and regulation.^{128,136,168} For instance, for what concerns precision farming innovations for the application of nutrients at the best rate, time and place, the high cost of technologies (e.g. detailed soil, GPS and drone mapping) and of obtaining information (e.g. weather and satellite data) has slowed adoption,¹²⁸ and therefore limited private sector companies in their capacity to scale technologies up for affordability.¹⁵⁶ Crucially, there is an intrinsic limit to the capacity of management and technology options to mitigate agricultural nitrogen run-off and especially livestock GHG emissions.^{136,137,148} At a global level, the mitigation benefits of improved grazing management (i.e. avoiding over-grazing and soil erosion) are greatly outweighed by the animals' direct GHG emissions,^{174,175} and there are physiological and agronomic limits to the extent to which GHG emissions from ruminants' enteric fermentation can be reduced through feed additives and manure management or herd management and breeding.^{135,137,172}

Even assuming that at the global, aggregate level the adoption of improved management practices and technologies is sufficient to raise total yields and avoid a net increase in farmland, the latter may continue to contract in temperate regions and expand in tropical regions.^{128,132} This would limit the potential for sustainable intensification to mitigate climate change, biodiversity loss and zoonotic disease risk. More generally, there is growing consensus that even in the most optimistic scenario of widespread uptake of the best available management and technology options, the huge challenge of feeding an increasing human population without compromising the Earth's ecological stability will not be overcome without a radical shift in human diets away from their current heavy reliance on livestock source foods.^{125,129,136,140,156,168,173,176,177}

A global shift to predominantly plant-based diets has therefore been identified as crucial to reduce GHG emissions^{129,136,137} and biodiversity loss.^{138,140} These diets, sometimes referred to as 'flexitarian diets', are informed by current evidence on healthy eating and characterised by large amounts of plant foods (fruit, vegetables, plant source proteins like pulses, nuts and seeds, wholegrains and unsaturated plant oils), modest amounts of animal source proteins (fish, poultry, eggs, dairy), low amounts of red meat (beef, lamb, goat, pork) and processed meat, limited amounts of saturated fats, added sugar, refined grains and highly processed foods, and a balanced energy intake.¹⁵⁶ As discussed in the previous section, such a dietary shift may contribute to also reducing the risk of wildlife-origin zoonotic disease outbreaks and EID

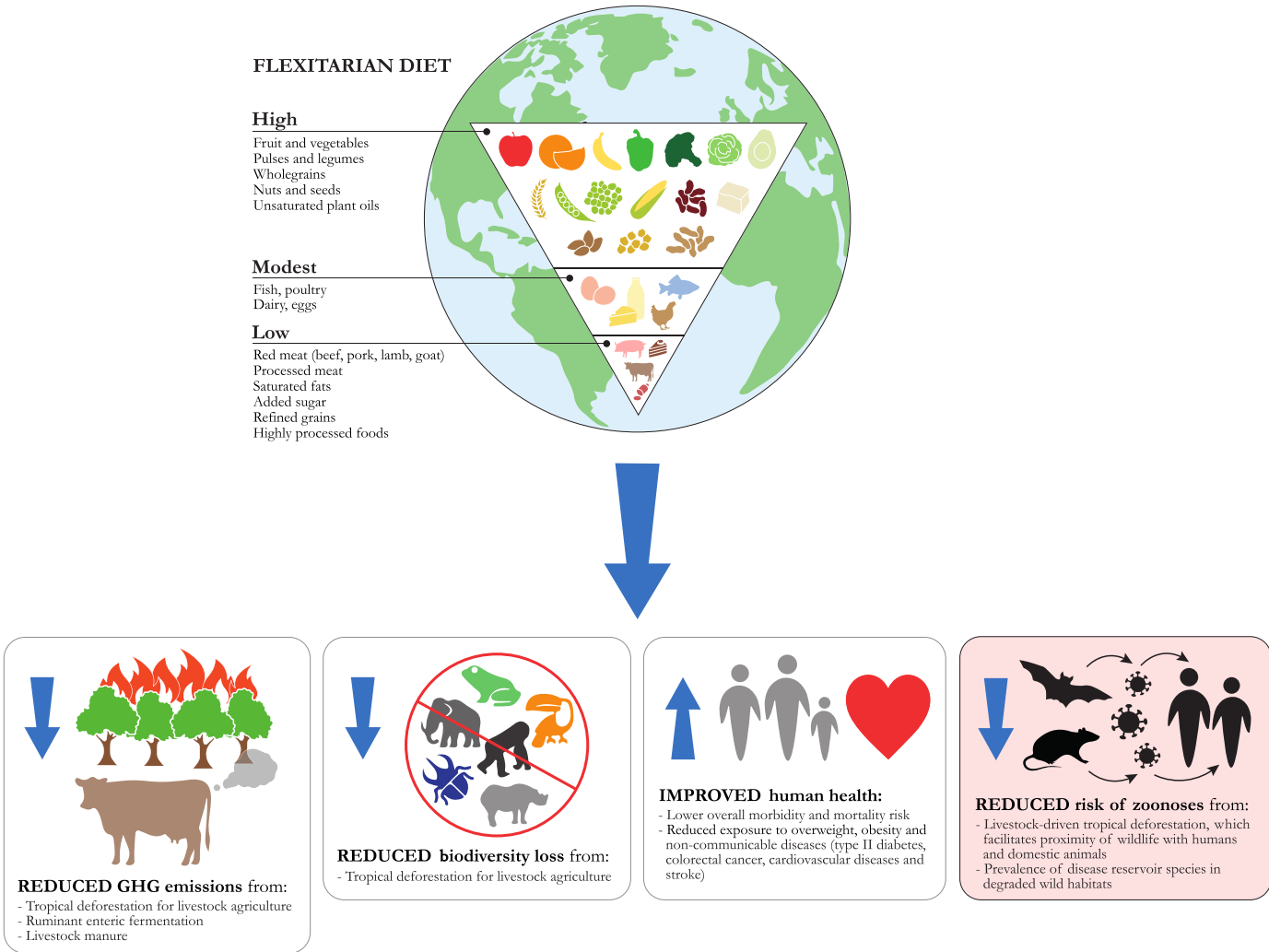


Figure 3. Benefits of a global shift to a plant-based (flexitarian) diet

events.^{76,106} In addition, a transition to more plant-based diets characterised by low shares of livestock source products would generate other important human health,^{22,156,163,178–182} agronomic and food security^{183–185} benefits (Figure 3) (see Webappendix 5. *The human health, agronomic and food security benefits of predominantly plant-based (flexitarian) diets*).

Predominantly plant-based, flexitarian diets have therefore been suggested as global reference diets for adults¹⁸². Such diets allow for adaptation to personal dietary needs, preferences and cultural traditions, and include diverse dietary patterns such as omnivore, pescatarian, vegetarian and vegan. The features of a flexitarian diet are well established in the traditional diets of several regions (e.g. the Greek Mediterranean diet of mid-20th century and the traditional diets of India, China, Mexico and West African countries), which are largely plant-based, high in vegetable sources of protein like soy and nuts and low in red meat and dairy foods.¹⁵⁶

Organic farming is one of the few legally regulated and internationally recognized approaches to sustainable agriculture that is known to deliver important local environmental benefits^{186–189} (see Webappendix 7. *Organic farming principles*). It is also a rapidly growing food sector – the fastest in European and North American countries.¹⁹⁰ As such, it is worth exploring whether there can be complementarities and synergies between policies promoting large scale conversion to organic farming and those pursuing a global shift to predominantly plant-based diets.

Organic farming has been widely reported to perform better than conventional farming against a range of environmental indicators, such as improved soil structure, biota activity and water holding and carbon sequestration capacities,^{191,192} reduced per unit area aquatic and terrestrial pollution from herbicide and pesticide leaching and nutrient run-off, and lower per unit area GHG emissions thanks to decreased production and use of synthetic fertilisers.^{186,188,189,191} Its more heterogeneous landscape features, together with decreased pressure from herbicides and insecticides and more diversified cropping practices, support a higher plant and animal biodiversity.^{187,193}

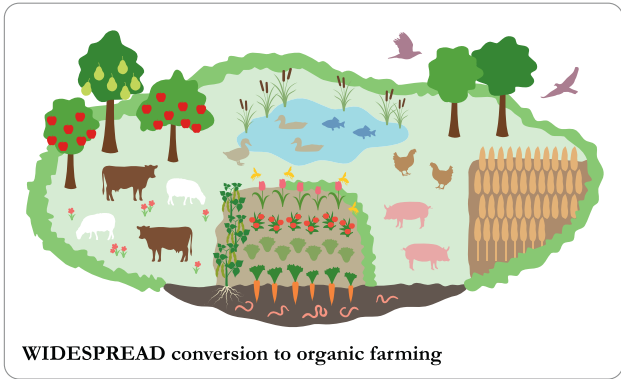
However, organic crop systems have an average 8–20% lower yield productivity than conventional systems,¹⁹⁴ and therefore tend to require larger stretches of land to produce the same quantity of product. Although at present only 1.4% of total global agricultural land is managed organically,¹⁹⁰ if large scale conversion to organic farming were to occur, this could be at the expense of ‘extensification’ onto new land.^{167,168} If farmland expansion were to occur onto natural habitats (rather than degraded and secondary habitats), it could greatly increase biodiversity loss,¹³³ GHG

emission,¹⁹⁵ eutrophication of natural ecosystems¹⁸⁴ and potentially zoonosis transmission rates.^{76,106,107} In fact, biodiversity loss and GHG emissions are significantly higher when the same increase in food production is pursued through cropland extensification onto natural habitat than through intensified application of synthetic fertilisers on existing agricultural land.^{133,195} In other words, although organic production systems generate comparative local environmental benefits, widespread adoption without changes in total demand can involve trade-offs due to new conversion of natural ecosystems to meet overall food demand,^{167,168} with such conversion potentially occurring abroad (the so-called ‘telecoupling’ effect).^{131,196}

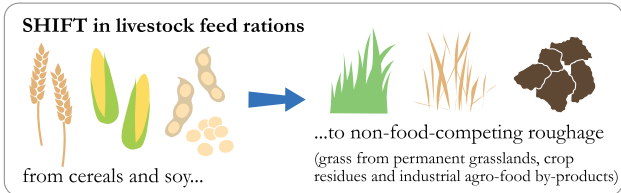
Yet, the pursuit of sustainability necessarily relies upon tackling both the production and consumption sides of food systems.^{127,136,197} Food system models^{176,198} suggest that complementing conversion to organic farming with a shift in livestock feed rations from cereals and soy to non-food-competing roughage (i.e. grass from permanent grasslands and by-products from food processing),¹⁹⁹ a reduction in livestock source food consumption¹⁹⁸ and cutbacks in food loss and wastage^{197,200} could feed more than 9 billion people in 2050 without additional farmland and with overall reductions in negative environmental impacts¹⁷⁶ (Figure 4). In fact, considering that land used for plant source food production generates many more calories per hectare than land used for livestock source food production, reducing consumption of the latter is the single most effective strategy to improve the productivity of the land.¹²⁹

Moreover, greater investment in the development of crop varieties and animal breeds better-suited to low-input organic systems,^{201,202} and in management practices that improve soil health (e.g. diversified and cover cropping, conservation tillage),^{173,194,203} address yield-limiting factors (e.g. improved organic pest control, the use of bioeffectors such as mycorrhiza or rhizobia),¹⁸⁹ and optimize nitrogen use efficiency and recycling (e.g. organic waste reusing)^{171,189} has the potential to significantly increase organic farming productivity. Recoupling cropping and livestock and allowing farm animals to graze on fallow land, as done in many smallholder²⁰⁴ and organic^{191,193} mixed farm systems, also offers a path to closing nutrient cycles, improving soil quality, raising land productivity and decreasing pollution from manure waste management.^{128,129,204} These yield-increasing measures would bring the further benefit of lowering the price of food produced through organic and other sustainable farming methods to levels that are closer to those of conventional farming and affordable also by less affluent segments of the population.¹²⁹

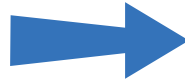
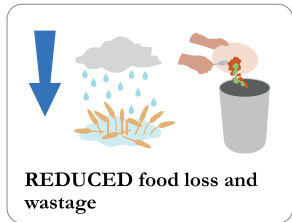
SUSTAINABLE GLOBAL FOOD SYSTEM



+



+



PLANET EARTH IN 2050



Figure 4. Global food system model complementing conversion to organic farming with a reduction in livestock source food consumption and cutbacks in food loss and wastage

Industrial-engineering crop farming approaches, such as soil-less vertical farming and crop-aquaculture, offer another mechanism to reduce agricultural extensification onto wildlands, by delinking food production from soil and natural environments while retaining its link to natural processes. These high-tech, capital-intensive options can be designed to maximise certain environmental sustainability targets such as closed nutrient cycling and recycling,^{205,206} and consumer acceptability may be less of an issue than generally assumed.²⁰⁷ However, their potential in terms of sustainable energy use and price competitiveness with conventional and organic farming is poorly known. Moreover, they are of limited relevance to poorer regions of the globe characterised by scarcity of capital and abundance of land.²⁰⁷

In developing countries that are rich in wildlands it is instead crucial that agricultural and land use policies continue to actively discourage livestock grazing and feed crop expansion from occurring onto natural and secondary habitats,^{151,198} directing such land uses towards lands that are already environmentally degraded such as abandoned agricultural areas and tree plantations. For example, in the Brazilian Amazon, between 2005 and 2012, reduced deforestation was successfully pursued through rural credit restrictions for counties with high deforestation rates, expansion of state protected areas and indigenous reserves in active agricultural frontiers, and Greenpeace-led embargos that excluded soy and beef grown on illegally cleared land from supply chains.²⁰⁸

Finally, in order to contain farmland expansion, major reductions in food losses and wastage across the food supply chain are also crucial; considering that at present more than a third of all food produced is either lost before it reaches the market or wasted by retailers, households and the hospitality industry.^{197,200} In rural areas of low- and middle-income countries, food loss at the initial production stages could be tackled through investment in improved harvest scheduling and techniques, post-harvest storage facilities, processing technologies (e.g. drying, packaging) and transport.²⁰⁰ Improvements are also necessary by the feedstock industry in their utilisation of crop residues, agro-industrial by-products and food waste.¹⁹⁹ In urban areas, food waste by the public could be addressed through shelf-life prolonging packaging, clearer best-before labels, awareness campaigns promoting purchase planning and storage practices, and waste recycling back into production. Food manufacturers, retailers and services could also reduce portions¹⁵⁶ (Figure 4).

Strategies for promoting a global transition to more plant-based diets

Promoting a global shift towards healthier and more environmentally sustainable plant-based diets is an

enormous challenge as consumer preferences for animal source foods are rooted in biological and socio-cultural factors.²⁰⁹ Meat consumption is part of the human evolutionary heritage,²¹⁰ and today, for a large share of the global population, the price of meat relative to income is lower than ever in history.¹⁴⁸ Moreover, surveys in the US and Australia suggest that people who consume relatively higher quantities of meat and other livestock source foods tend to be generally less sensitive to ethical concerns in their food choices.²¹¹

Nonetheless, consumption habits and norms can and do change. This is indicated, for example, by dietary transitions from beef to pork and chicken in the US, Europe and other regions – which are partly a consequence of changes in their relative price,²¹² and the growing numbers of organic,¹⁹⁰ restricted omnivore, vegetarian and vegan consumers^{213,214} in high-income countries – which are partly associated with rising concerns for environmental sustainability and farmed animal welfare.^{215,216} These trends can be further encouraged through coordinated initiatives by government, civil society and the private sector.¹⁴⁸ Governments that dodge interventions to discourage unsustainable levels of livestock source food consumption for fear of public backlash may be overestimating such risk, as suggested by public expectation of government leadership in tackling this complex problem.^{129,217}

Obviously, current levels of consumption of livestock source foods and the degree of reliance of human communities on animal source proteins differ across countries and geographical regions. Efforts to reduce livestock production should prioritise excessive consumption levels in wealthier countries^{144,156} and in the expanding metropolises of developing countries.^{146,218} On the contrary, communities inhabiting harsh climates and marginal lands that are inhospitable to crop cultivation. On the contrary, communities inhabiting harsh climates and marginal lands that are inhospitable to crop cultivation – such as hunter communities in tropical rainforests,^{100,219} Inuit communities in Arctic regions^{210,220} and pastoralist communities in arid and semi-arid rangelands²²¹ – will necessarily continue to rely conspicuously on animal source foods for nutrition (Figure 5) (see Webappendix 6. *Animal source food consumption levels across different socio-economic and ecological contexts*).

In regions characterised by high levels of consumption of livestock source foods, the available evidence indicates that providing consumers with information about the health and environmental impacts of food without additional contextual changes and regulatory or fiscal measures has limited effectiveness.^{222,223} In order to initiate a dietary transition away from heavy reliance on livestock source foods, the best strategy may therefore be to couple ‘soft’ informational and contextual interventions to raise consumers’ awareness and

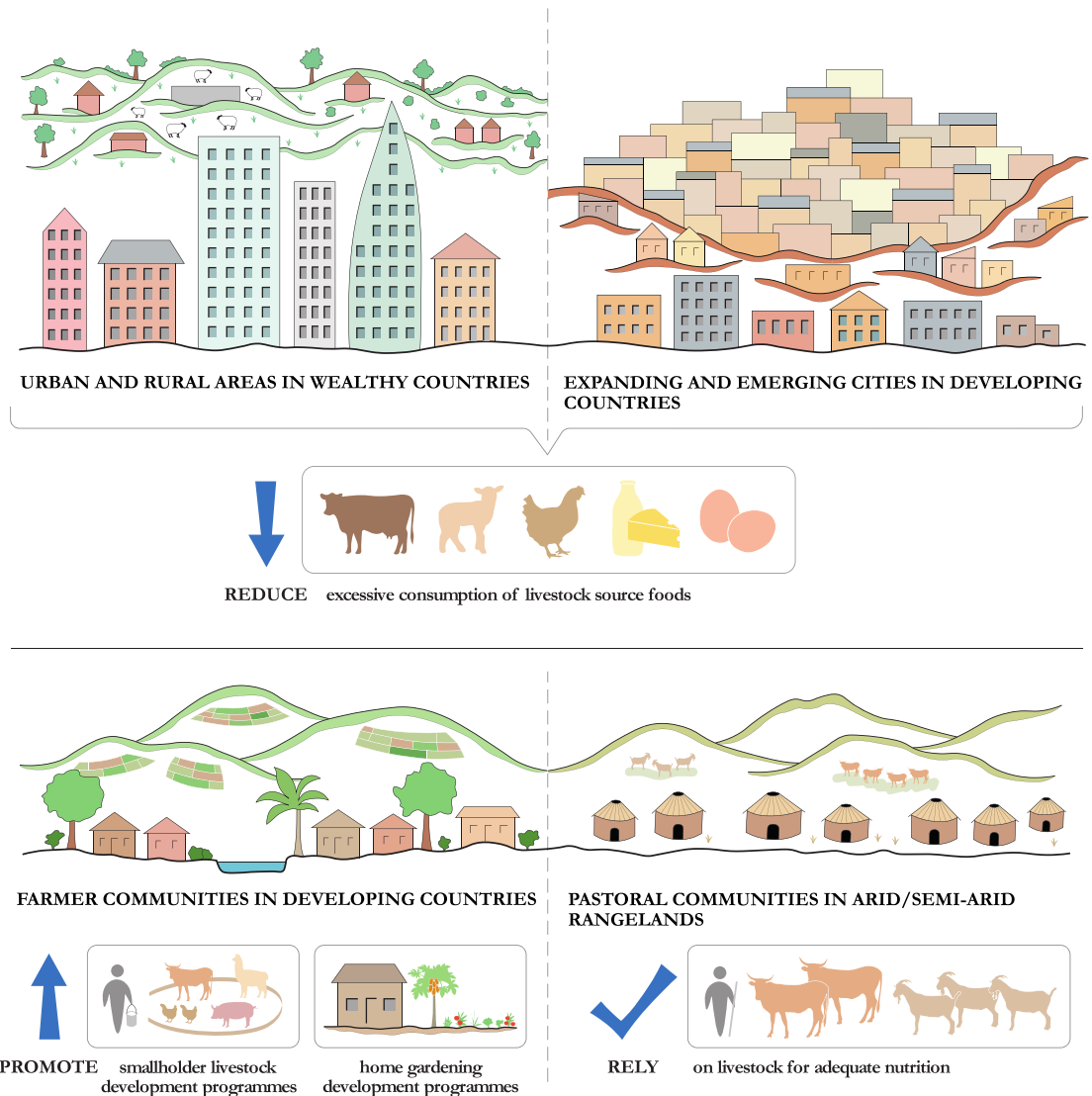


Figure 5. Approaches to sustainable livestock source food consumption in different geographical regions

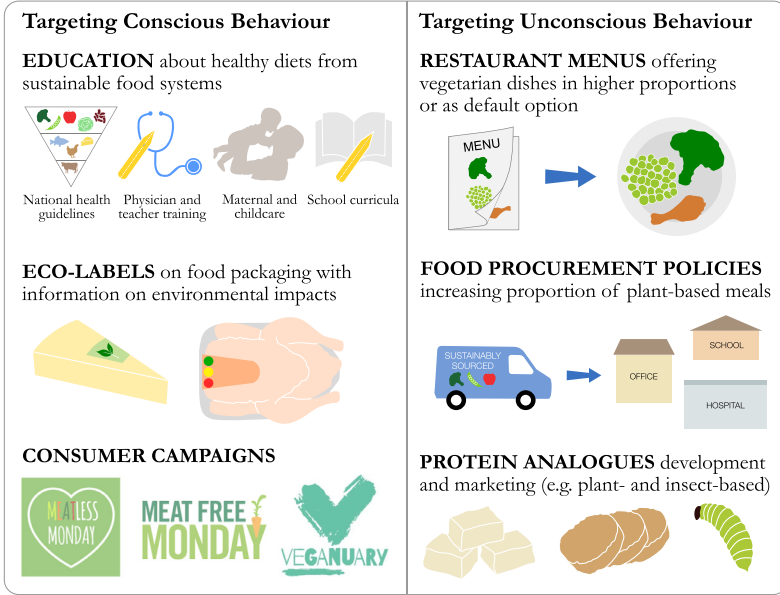
‘nudge’ them towards dietary changes, and ‘harder’ fiscal measures towards which public resistance may progressively wane as people become increasingly aware of the risks of inaction and familiar with alternative dietary patterns^{148,222,224} (Figure 6). In fact, even when awareness and education are unlikely to produce major or sustained change in consumer demand for livestock source foods, they may still be an important precursor to harder regulatory measures and necessary to catalyse public support for policy change.^{147,225}

An important first step in this direction would be to better align national dietary guidelines, including those offered by paediatricians to families, with current evidence on healthy and environmentally sustainable diets.¹⁸² Targeting the young through education may be particularly important, since food tastes and eating habits tend to

develop during the first years of life and to be persistent.¹⁵⁶ To be enduring, education on healthy diets from sustainable food systems need to be integrated into maternal and childcare programmes, and into compulsory school curricula and textbooks.^{129,156} Training and clinical practice of physicians and paediatricians also need to include nutrition and ecosystem stability as determinants of human health^{156,224} (Figure 6). In Japan and South Korea, for example, diets remain higher in fish and plants and lower in meat and sugary drinks than in most developed countries, thanks to policies such as compulsory school lunches, government-funded lessons on traditional food preparation and strong campaigns promoting traditional cuisines.²²⁶

Tested informational and contextual interventions include front-of-pack eco-labels with simplified

SOFT MEASURES



Soft strategies may catalyse public support for policy change toward harder regulatory measures

HARD POLICIES

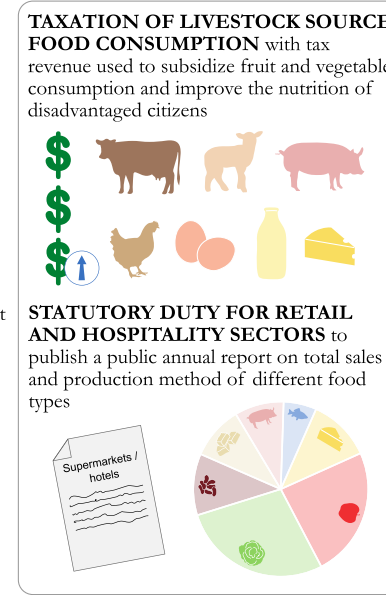


Figure 6. Strategies to promote a dietary transition away from heavy reliance on livestock source foods

information on environmental impacts, which have been observed to encourage some consumers to shift towards more sustainable food choices.^{227,228} Campaigns such as the Meatless Monday and Veganuary have also had some success; through a ‘foot-in-the-door’ psychological technique, these initiatives enable consumers to commit to a small dietary adjustment with the possibility of later developing a desire for greater change, and also encourage businesses to launch new plant-based products and menu options²²⁴ (Figure 6).

Other interventions rely on unconscious behavioural responses to contextual cues. For instance, increasing the proportion of vegetarian meals offered at cafeterias,²²⁹ and programming restaurant menus and online meal registrations²³⁰ by offering vegetarian dishes as a default option, can increase the number of people choosing them.

The retail and hospitality sectors could be enticed to use their potent customer-choice influencing skills and enormous purchasing power to stir consumers and producers towards more environmentally sustainable and healthy foods. Such enticement could come from a statutory duty to publish an annual report open to public scrutiny on total sales of fruit, vegetables, plant source protein and livestock source foods together with their method of production accreditation (e.g. organically grown, pasture-fed, sustainably fished).¹²⁹ Food procurement policies could also promote a higher percentage of plant-based, sustainably sourced meals at workplaces, schools, hospitals, barracks and prisons – when food is produced in bulk quantities, small changes (e.g. including minced mushrooms in beef burgers) can have large environmental and health impacts^{129,156,224} (Figure 6).

Moving on to fiscal policies, proposals have recently been made to tax livestock source foods not only to mitigate their environmental impacts, but also to account for the financial burden of meat-related chronic diseases borne by public health systems^{224,225} (see Webappendix 5. *The human health, agronomic and food security benefits of predominantly plant-based (flexitarian) diets*) and for the risk of zoonosis outbreaks involved in their production.²³¹ In reality, efforts to fiscally regulate agricultural production to mitigate environmental impacts such as climate change have so far been limited in comparison to other sectors such as transport, energy, steel and cement,²²⁴ for several reasons. First, compared to other polluting industries, in agriculture the fonts of GHG emissions (e.g. crop residue decay, ruminants’ enteric digestion) are diffuse and highly variable and therefore difficult and costly to monitor.²³² Second, agricultural GHG emissions associated with biological processes that are intrinsic to crop and livestock production (e.g. methane from flooded rice paddies and ruminants’ digestion) cannot be easily addressed by producers through technological and management mitigation options in response to taxation.^{135,157,172} Third, taxing food

production for GHG emissions may penalise domestic products versus imported ones,²²⁴ unless arduous multilateral agreements for the regulation of meat and dairy supply are established.²³³

Therefore, although taxation works best if targeted to the intended externality at source, taxing consumption rather than production of livestock source foods is considered a more practical strategy (Figure 6), and some modelling studies have been carried out.²¹⁷ One such study indicates that levying GHG taxes on the consumption of livestock source foods worldwide could reduce food-related emissions by about 9%. A portion of tax revenue would be available to compensate poorer consumers in low-income countries, who spend a larger proportion of their income on food, for potential budget losses. In this study, the mitigation potential of consumption-side GHG taxation measures compares favourably to that of supply-side measures like improved feed additives and manure management.²³⁴

The potential effectiveness of internalising external environmental and public health costs through consumption taxes warrants detailed assessment in specific jurisdictional contexts.²³⁵ A key factor is the price elasticity of taxed products, i.e. how strongly the quantities produced or demanded react to increases in price. For example, health-related taxes targeted at sugar-sweetened beverages^{235,236} and energy-dense²³⁷ and high-saturated fat²³⁸ foods have been observed to encourage food companies to reformulate and consumers to reduce consumption of these products, including a limited decrease in the consumption of certain beef and dairy products.²³⁹ In some countries, these taxes are estimated to have resulted in reduced cases of obesity and decayed and missing teeth.^{129,236} Yet, the environmental and health outcomes of such taxes critically depend on the cross-price elasticity of demand of other environmentally impactful and/or unhealthy products, and can be partly offset by consumers shifting their shopping to non-taxing jurisdictions.^{235,238}

It is also important to avoid the potential unintended consequence that low-income households may respond to a rise in price of environmentally impactful and/or unhealthy foods by cutting back further on healthy foods such as fruit and vegetables. State taxation revenue could therefore be used to subsidize fruit and vegetable consumption,²³⁴ or invested in programmes for improving the nutrition of disadvantaged segments of the population.²¹⁷ Examples of the latter include school free meals and holiday food clubs, vouchers for fresh fruit and vegetables for pregnant women and pre-school children, community initiatives (e.g. farmer markets, box schemes),¹²⁹ and legislation that enables doctors to prescribe vouchers for fresh fruit and vegetables and government-funded

classes on nutrition to people suffering from diet-related chronic health conditions.²⁴⁰

Taxation of livestock source foods, whether at the producer or at the consumer level, must also address likely challenges in terms of social acceptance.²³¹ In most countries, livestock source food production, processing and retailing are conspicuous economic sectors with strong vested interests and political influence.^{148,233} Meanwhile, given widespread and strong consumer preferences for livestock source foods, the degree to which the state should intervene to limit their consumption for public health and environmental objectives is subject to controversy.^{148,224} Yet, in a recent public poll in England, a country with a strong meat and dairy culture, 62% of participants were either in favour or not opposed to the introduction of a tax on fresh and processed meat.¹²⁹ An experimental study also indicates that in advanced economies, consumers' support for a moderate consumption tax on livestock source foods could be enhanced by bundling it with popular policies such as enforcing stricter environmental standards on livestock farms and discounting plant-based alternative protein foods.²¹⁷ One way to ease opposition by livestock farmers, on the other hand, may be to use the revenue obtained from consumption taxes to reward them for on-farm activities that further enhance the targeted ecosystem services (e.g. restoration of natural habitat for carbon sequestration and nutrient run-off regulation).²⁴¹

Finally, over the past decade there has been significant investment in the development and marketing of meat, dairy and seafood protein analogues, including plant-based substitutes (both traditional and highly processed ones), cultured meats and edible insects^{242,243} (Figure 6). By decreasing land conversion that is primarily driven by demand for livestock source foods, these protein alternatives could contribute to reducing both environmental degradation and zoonotic spillover risk. However, these products vary significantly in their current and potential capacity to limit land conversion and other environmental impacts, and in their health benefits and consumer acceptability^{243–247} (see Webappendix 8. *Protein analogues – opportunities and challenges*).

Wild meat bans can be counter-productive for curbing trade and zoonotic disease risk

In tropical and subtropical regions, wild meat plays a crucial role in local livelihoods and food security,^{97,100,150,219,248,249} especially during periods of environmental and socio-economic crisis.^{99,250–252} In the past three decades, wildlife conservation policies

have therefore been reframed around the principle of sustainable harvest and trade of wild animals and plants in order to accommodate the nutritional and livelihood needs of IPLCs.²⁵³ Social research culminating in the United Nations Sustainable Development Goals (SDGs) has highlighted the central economic and cultural role of wild meat for IPLCs.²⁵⁴ The 2016 Resolution on CITES (the Convention on International Trade in Endangered Species) and Livelihoods further recognized that building livelihoods from sustainable wildlife uses can contribute to the conservation of species and ecosystems.²⁵⁵

In recent years, though, the public health threat posed to an increasingly interconnected world by zoonoses of suspected wildlife-origin like HIV/AIDS, Ebola, SARS and most recently COVID-19 has raised new challenges for the fragile policy balance between local livelihood needs and global conservation priorities. During the 2013–16 Ebola outbreak in West Africa and in the early days of the COVID-19 pandemic in China, several animal welfare and wildlife conservation NGOs made calls for national governments and the World Health Organization (WHO) to forbid commercial wild meat trade.^{85–88} A primary component of public outbreak control measures was either the proscription of wild meat trade and consumption (e.g. in Sierra Leone and China),^{89,256} or the issuing of strong information campaigns linking wild meat to zoonoses (e.g. in Nigeria, Côte d'Ivoire, Cameroon).²⁵⁷ These events reignited debate over the effectiveness and acceptability of banning tropical wild meat hunting and trade for public health and conservation goals.^{85,258,259}

However, blanket bans on wild meat can be problematic for a number of reasons. Firstly, as mentioned above, in many tropical and subtropical regions of Africa, Asia and South America, wild meat hunting and trade enables rural populations to meet their basic nutritional and income needs.^{100,150,220} For IPLCs in remote forest areas with little access to affordable domestic meat and fish, wild meat is often the main source of protein, fats and micronutrients.^{97,98,100} In the Congo and Amazon rainforest basins, for example, wild meat consumption satisfies between 60–80% of daily protein needs.^{150,219} In remote rural communities where economic opportunities are scarce, wild meat trade also makes important contributions to household income.^{248,249} In rural areas and provincial towns where it is not the primary source of protein, wild meat may still constitute a vital safety net during emergencies such as drought, epidemics, economic crisis and violent conflict.^{99,250–252} A blanket ban may have particularly negative impacts on poorer rural households who depend on wild meat for a large share

of their protein intake and income generation.^{248,249} For many IPLCs, hunting and consumption of wild meat has been part of their livelihood for centuries and is an important constituent of their culture and identity.^{220,249,260}

Secondly, bans are often futile and can even be counterproductive for reducing wild meat trade. The effect of a trade policy – be it a trade ban or trade regulation – on wildlife prices, demand and illegal supply is an empirical matter, influenced by wildlife biological and ecological features, market characteristics, and state enforcement and monitoring capacities that vary depending on the species, market segments and geographical locations involved.^{261,262} To be effective in stopping hunting and preventing the emergence of black markets, a trade ban requires extensive state enforcement and monitoring capacity, which in tropical and subtropical developing countries characterised by weak state institutions²⁶³ tends to be low.^{91,93} In developing countries, wildlife law enforcement is also particularly susceptible to corruption,^{264,265} with enforcement authorities turning a blind eye to illegal hunting for bribes, or reselling the seized wild meat to private clients.²⁶⁶ This is partly due to the low importance generally granted to wildlife crime compared to other forms of crime,²⁶⁷ and the small and irregular salaries received by wildlife and law enforcement officials²⁶⁸ (although there is encouraging evidence from other sectors that corruption can be reduced at the country and local project level).^{265,269}

Thirdly, consumer preferences for wild meat are shaped not only by its price and household wealth, but also by non-price determinants (e.g. taste preferences, perceptions of healthiness, familiarity with protein substitutes, associations with tradition and social status) that constrain its price elasticity of demand.^{95,96,270} Where the non-price drivers of wild meat demand are strong, a trade ban that reduces supply and increases prices may fail to discourage consumption.^{91,92,96} In some cases, increased rarity and price may even raise the social status of consuming wild meat and consequently drive up demand.^{94,95} Further, some cases of species up-listing from CITES Appendix II to Appendix I have led to spikes in legal trade in the months prior to the ban taking effect – a factor that has caused serious exploitation for species like Kleinmann's tortoises and Geoffroy's cats.²⁷¹ These considerations indicate that in the absence of effective law enforcement and demand reduction campaigns, a trade ban may fail to reduce and may even encourage illegal wild meat trade.

Fourthly, a blanket ban criminalises unregulated but sustainable forms of wild meat hunting and trade that target smaller, fast reproducing species (e.g. large rodents, pigs, small ungulates) that can withstand intensive hunting, and which can be important for local food security.^{272,273} In West and Central Africa, these species comprise up to 70% of subsistence hunting and trade.^{150,274} In several African countries,

African giant pouched rats and cane rats are not only highly appreciated as food, but their harvest is also regarded as a form of pest control.⁷¹ A blanket ban would also undermine sustainable wild meat farming enterprises that in some parts of the tropics have substituted harvesting from the wild and contributed to the recovery of species like the capybara in Brazil,²⁷⁵ crocodiles in Africa and Central America²⁵⁵ and sea turtles on the Cayman Islands.²⁷⁶

Fifthly, tightening restrictions on local wild meat uses without enacting effective anti-corruption strategies and implementing wider policies of rural development that enable IPLCs to engage in alternative livelihoods, can alienate IPLCs and further entrench the divide between them and conservation authorities. In this way, blanket wild meat bans can be unfavourable to long term wildlife conservation goals.^{101,102}

Finally, and crucially, a wild meat ban risks being counterproductive in both reducing the risk of emergence and re-emergence of wildlife-borne zoonoses, and in controlling human contagion once spillover has occurred. By forcing trade underground, a ban might encourage the proliferation of illegal wild meat markets where less attention is paid to biosecurity measures that are important to prevent zoonotic spillover.^{89,103,258,259} Wild meat traders and consumers might also be less likely to report illegal wild meat market transactions in outbreak investigations.

Once a virus has entered a human population and has adapted to its new human host, a wild meat ban cannot contain contagion that is driven by human-to-human transmission rather than by repeated contact with wild animals or their meat.²⁷⁷ Likewise, the risk of disease spreading to new areas lies with the movement of infected people, rather than the trade of infected wild animals and meat. For example, the unprecedented scale of the 2013–16 Ebola outbreak in West Africa has been linked to higher human population density and mobility compared to the more remote areas of Central Africa affected by previous outbreaks.²⁷ A focus on wild meat prohibition may detract public attention from the more critical causes of interpersonal contagion, such as contact with infected people and perilous burial practices.^{278,279} In areas where wild meat is central to food security and livelihoods, a ban can also erode public confidence in government outbreak control measures. In these ways, a wild meat ban risks undermining the efficacy and legitimacy of government outbreak responses.⁸⁹

Strategies to curb tropical urban wild meat demand while securing access for Indigenous Peoples and Local Communities (IPLCs)

In tropical regions, wild meat hunting and trade is increasingly driven by urban demand. In some large cities of the Congo and Amazon basins, although wild meat provides

a minor proportion of per capita protein consumption, aggregate demand is very large.^{149,150} In many Asian countries, wild meat consumption is considered to symbolise high social status because of its relative rarity, cost and association with old elites, so that growing prosperity among the urban middle class has driven a rapid increase

in wild meat demand.^{95,280} Considering that in most established metropolises of tropical regions, legume, fish and livestock source proteins are available in ample supply and at affordable prices, here wild meat consumption is no longer a nutritional necessity, but is rather driven by taste preferences, perceptions of freshness and

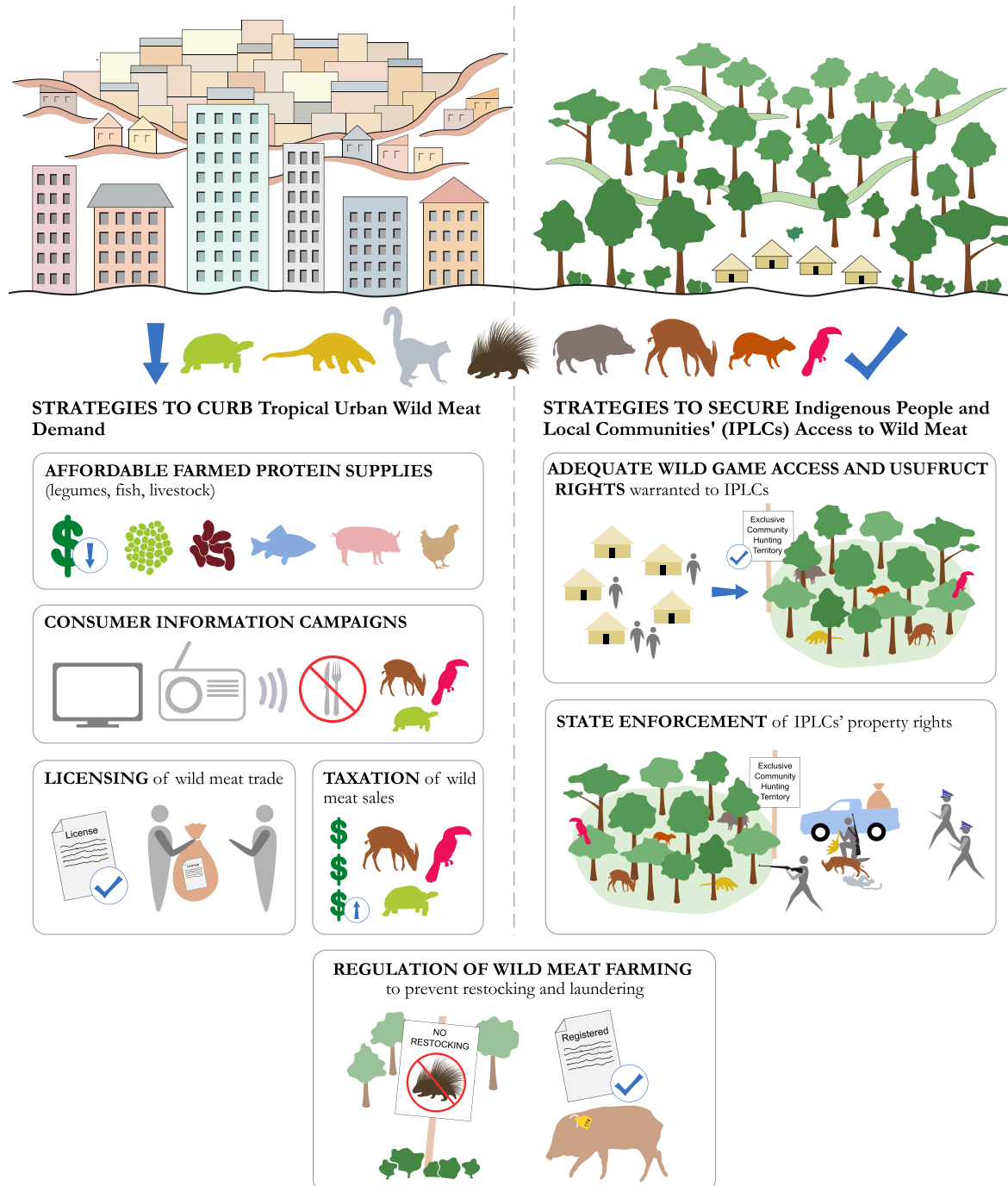


Figure 7. Strategies to curb tropical urban wild meat demand and secure indigenous people and local communities' (IPLCs) access to wild meat

healthiness, cultural motivations or associations with social status and prestige.^{95,96,270}

Supplying cities with wild meat from tropical forests is not ecologically viable.^{149,150} In livestock-grazed rangelands where predators (e.g. dingos and wild dogs in Australia) have been partially removed and permanent water supplies have been expanded, commercial hunting of large wild herbivores (e.g. kangaroos) for their meat acts as a strategy to control total grazing pressure and preserve landscapes and biodiversity.²⁸¹ The situation is starkly different in tropical and subtropical forests. Here, the interaction of the intrinsic low productivity of large wild herbivores²⁸² with widespread loss of continuous habitat and large and growing urban populations means that even very low urban per capita consumption rates can result in an aggregate urban demand that would outstrip sustainable wild meat harvesting in the surrounding areas.^{149,150} In Kinshasa, for instance, consumption of only 1 kg of wild meat per inhabitant per year can result in massive wildlife harvests when multiplied by its 8 million residents.⁷¹

Consequently, in tropical regions the present scale of urban wild meat demand simultaneously threatens biodiversity^{68,96} and the food security of wild meat-reliant IPLCs.^{97,283} In addition, high levels of urban wild meat consumption may increase the risk of wildlife—human zoonotic disease transmission by incentivising hunter penetration of pristine forests,^{71,284} expansion of wildlife farming enterprises^{285,286} and increased wild meat sales in urban and peri-urban markets.^{287,288} A large and expanding wild meat sector poses a substantial strain on state capacity to enforce biosecurity measures and carry out disease surveillance.²⁸⁹

A balanced approach to tropical wild meat hunting and trade, addressing zoonotic disease threats and biodiversity losses while preserving local livelihoods, requires a holistic strategy that supports sustainable and biosecure wild game management in rural subsistence areas and curbs wild meat demand in established metropolises and emerging provincial towns where alternative protein sources are available or can be established^{71,249,254} (Figure 7).

The few existing community-based wild game management initiatives indicate that local communities can have noticeable ecological knowledge on sustainable hunting, and strong incentives to respect internal hunting rules^{253,290} and carry out anti-poaching monitoring on their territories.^{291,292} However, in many tropical countries IPLCs often lack secure land tenure and adequate wildlife usufruct rights,^{101,293,294} which undercuts their incentive and capacity to undertake effective wild game management.^{295,296} In many of these countries, national laws on community hunting either criminalize most local wild meat hunting practices (e.g. with respect to target species, offtake

levels, hunting areas, equipment), or are unclear about what forms of wild meat subsistence hunting and small-scale trade are permitted and by whom.^{71,294,297} The fact that many wildlife conservation groups continue to ascribe to a protectionist paradigm that views wild meat subsistence hunting and small-scale trade by village dwellers as inherently incompatible with wildlife conservation poses a further obstacle to the development of effective regulatory systems for sustainable community-based wild game management.^{248,297}

A first priority is therefore to warrant communities in remote, wildlife rich areas with exclusive access rights to game on their customary lands and to entrust them with locally relevant usufruct and management rights.²⁹² Adequate state enforcement of community property rights is also essential; without such backing, local communities may be unable to prevent outsiders from hunting illegally in their territories and may be exposed to violent attacks^{295,298} (Figure 7). As a starting point, state law enforcement capacity could be increased by investing in improving the proficiency of police, legal and judicial personnel in wild meat hunting and trade laws.⁷¹

Community-based wild game management institutions could also be used to introduce biosecurity measures for safer wild meat hunting and handling among local inhabitants (see section 8 below).

Community-based initiatives can only be successful at promoting sustainable and biosecure wild game management on community lands if accompanied by efforts to reduce pressure from urban demand.^{150,286} To start with, in the growing number of settlements and provincial towns emerging near extractive, plantation and infrastructure construction sites, affordable supplies of locally farmed or imported legume, fish and livestock protein should be established or strengthened²⁹⁹ (Figure 7).

The next policy option to stem urban pressure would be to regulate the wild meat sector through a state-run trade license system that sets total wild meat offtake levels and permitted hunting zones and seasons. A parallel action would be to increase urban prices through sales taxation. However, in tropical and subtropical forest regions, regulation of the wild meat sector through trade licencing is extremely challenging due to high demand from large metropolises, the large number of rural and urban dwellers engaged in this commerce and the wide range of game species involved. States lack the resources and capacity to effectively regulate and monitor such trade, so that wild food harvesting and trade largely remains an informal, unregulated sector.^{71,96} Implementing a wild meat sales taxation system tends to be cost-ineffective and is similarly constrained by insufficient technological infrastructure and human resources.⁷¹ Moreover, since the non-price drivers of wild meat

demand (e.g. taste, perceptions of healthiness, cultural identity, social status) tend to be strong among urban consumers, consumption by relatively affluent households may continue even when prices are raised through taxation and/or protein substitutes are made available at affordable prices.³⁰⁰

It is therefore likely that information campaigns are necessary to tackle urban wild meat consumption, and need to precede or accompany other policies attempting to regulate or tax the sector and fight the corruption of enforcement officers. Depending on what demand drivers and market segments are targeted, consumer campaigns might focus on the presence of preservative chemicals and the risks of spoilage and zoonotic disease transmission in wild meat,^{252,301} they might portray domestic and other meat substitutes as more modern/fashionable choices,²⁴² or they might highlight the destructive impact of illegal wild meat trade on biodiversity and IPLCs (Figure 7). However, except for few studies,^{149,302} up to now it has been difficult to assess and draw lessons from wild meat consumer campaigns, as impact assessment has rarely been factored into their design.³⁰³

As mentioned in the previous section, not all forms of urban wild meat consumption pose sustainability threats. Some agricultural landscapes that have already lost much of their biodiversity, and are now mostly inhabited by fast-breeding, hunting-resilient species like large rodents, pigs and small ungulates, appear capable of supporting long-term wild meat urban trade even in the absence of strictly enforced hunting license and sales taxation systems.^{272,273}

Wild meat farming has also rapidly expanded as a strategy to satisfy urban demand and so reduce pressure on wild animal populations,^{285,304} with some success cases.^{255,275} However, wild meat farming projects often suffer a low adoption rate among rural communities or struggle to reduce hunting from the wild.^{286,301} This is due to a number of challenges, such as: the unsuitability of some wild animal species to captive rearing, which encourages farm restocking through wild-caught individuals; the lower cost-efficiency of wild meat farming compared to hunting, whereby farmers charge higher prices than hunters;^{301,305} the difficulty for farm-reared wild meat to satisfy urban consumer preferences;^{95,305} and insufficient state capacity to prevent laundering of illegally hunted wild meat into legal farm-reared wild meat markets.^{71,286} Therefore, in order to contribute to reducing hunting pressure on wild populations, wild meat farming initiatives need to be informed by an in-depth understanding of consumer responses to farm-reared substitutes, and the sector must be effectively regulated to prevent restocking from the wild and laundering.^{95,286,301}

Finally, in order to avoid becoming hubs for zoonotic disease outbreaks, legalised wild meat farms, abattoirs

and markets need to comply with biosecurity measures discussed in the next section.

Improving biosecurity along animal source food supply chains and other strategies to break zoonosis transmission pathways

A more balanced approach to tropical wild meat hunting, farming and trade – acknowledging its contribution to local livelihoods and promoting biosecurity measures along supply chains – may not eliminate the risk of endemic and novel zoonotic disease transmission altogether, but neither will an ill-conceived anti-wild meat campaign that is likely to shove these activities deeper underground and erode public confidence in government outbreak control measures.^{89,258}

In developing countries, wild meat hunters, farmers and butchers are highly exposed to bites and scratches from wild animals.³⁰⁶ Yet, those engaged in these occupations rarely perceive them to be hazardous, since they have been carried out for generations while information about potential zoonotic infection risk has been lacking. Moreover, many individuals engaged in wild meat hunting and trade perceive safety from zoonotic disease risk as a lower priority than earning a living from one of the few livelihood options available to them.³⁰⁶ In order to improve biosecurity in rural communities, interventions therefore need to focus on more than raising awareness about wild meat pathogen transmission; they should also provide local hunters, traders and butchers with training on safer ways to handle live and dead animals and inexpensive biosecurity measures that they can easily adopt to avoid infection.²⁸⁹

Biosecurity measures to prevent zoonotic disease transmission while hunting, butchering and handling wild animals and their meat include: wearing protective clothing (e.g. boots, long trousers and long-sleeved shirts – as many resist latex gloves for being slippery, flimsy and cost-prohibitive);²⁸⁹ averting bites by wild animals; avoiding the collection of dead or dying animals; wrapping recent kills in plastic or banana leaves to prevent animal blood from getting in contact with small cuts or micro-abrasions; washing hands regularly with soap and clean water; properly storing and preserving carcasses; preventing peridomestic animals (e.g. feral dogs) from frequenting slaughtering locations and eating carcasses; keeping children away from butchering and cooking areas and from playing with dead animals; and thoroughly cooking wild meat before eating^{307,308} (Figure 8). Yet, seemingly simple measures like these can still be challenging in low-resource rural settings where even

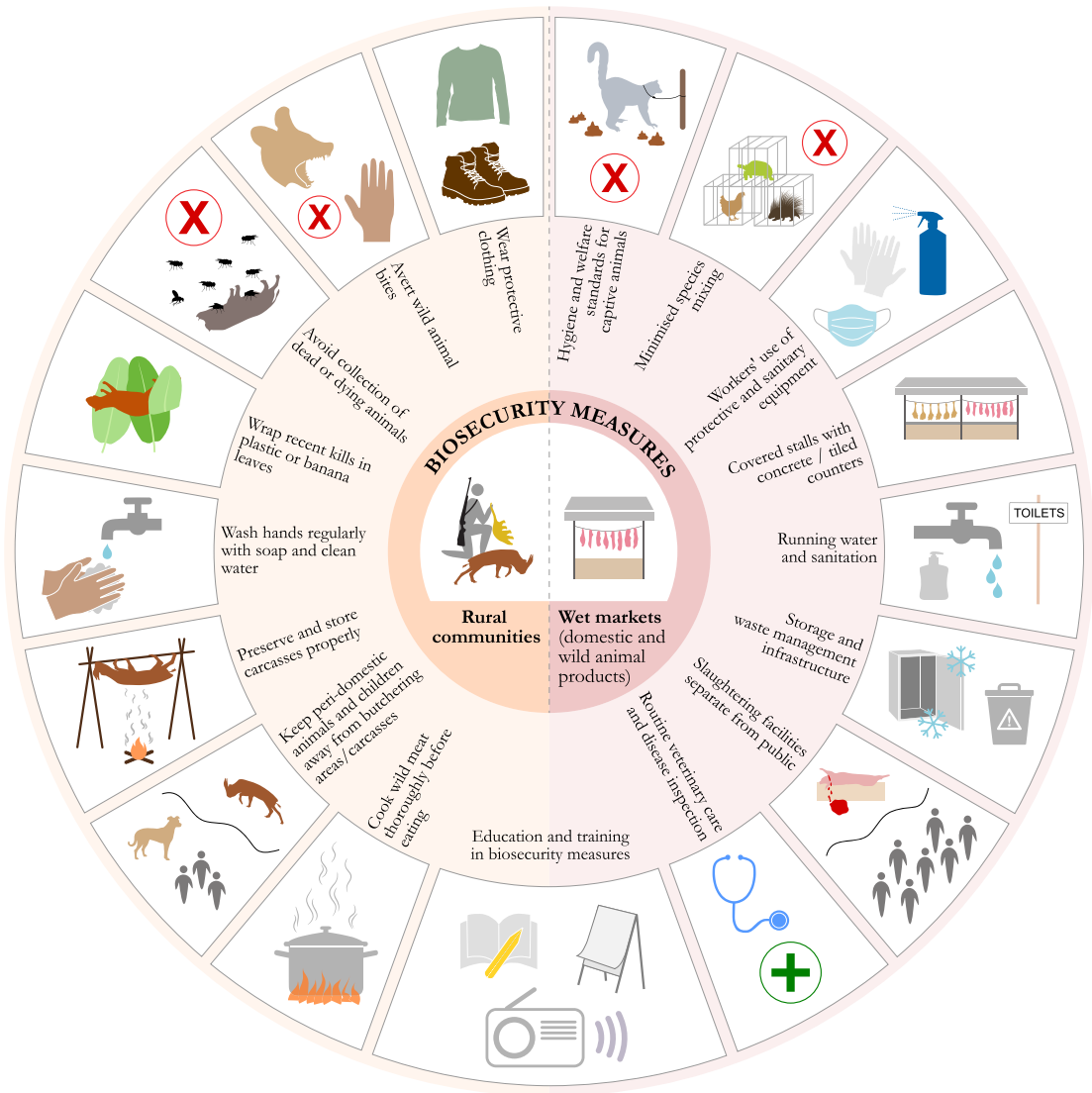


Figure 8. Biosecurity measures for hunting and handling wild meat in rural communities and in ‘wet markets’ selling domestic and wild animal products

access to clean water and basic storage facilities may be problematic.^{289,309}

The trade-offs experienced by local communities between livelihood benefits and disease risk from wildlife resource use highlight the importance of involving such communities in the design of biosecurity strategies.^{53,310} Educational messages also need to reach rural and urban dwellers in the informal or illegal wild meat trade, for example through text messaging, radio and poster campaigns.²⁸⁹

Wild meat hunting is not the only pathway for wild-life-origin infectious disease emergence and

transmission; instead, it is crucial that biosecurity measures are taken along the whole animal source food supply chain, including livestock and wildlife farms, animal transportation systems, abattoirs, food markets and restaurants.^{6,9,73} These measures include ensuring animal captive conditions that meet hygiene and welfare standards,^{256,288} minimising species mixing, worker use of protective and sanitary equipment, and routine veterinary care and disease inspection^{6,311} (Figure 8).

‘Wet markets’ selling fresh produce, including live or freshly slaughtered animals, underpin the informal food systems of fast growing rural and urban

populations in tropical and subtropical regions.^{287,312} Given the tendency of governments to discourage wild meat trade in favour of wildlife conservation, provision of market infrastructure such as covered stalls and concrete/tiled counters, running water, drains and overnight and cold storage is generally lacking for this sector, with the consequence that wild animals and their meat are handled under particularly unhygienic conditions.^{289,309} Governments should proactively invest in providing markets with adequate water, sanitation, storage and waste management infrastructure, stalls with surfaces that can be easily disinfected, and possibly slaughtering facilities that are separate from the public. Local government agencies should provide suppliers and retailers with training in biosecurity regulations and monitor compliance^{66,313} (Figure 8). As these markets play an important role in the diet and livelihood of millions of low-income rural and urban dwellers,^{287,312} it is important that the introduction of new biosecurity standards does not disrupt their access to these markets. ‘Top-down’ biosecurity measures that do not take into account the interests and norms of these local actors also risk being ineffective.³¹⁴ Hunters, farmers, traders, vendors, market managers, local administrators and public health scientists should therefore collaborate to identify locally-apt biosecurity regulations.⁶⁶

Physical distancing measures should also be adopted on farms, pastures, abattoirs and live animal markets to reduce zoonosis transmission.⁸⁴ For example, fencing is used to reduce bison—cattle contacts for brucellosis prevention.³¹⁵ In Malaysia, policies requiring that fruit trees are planted at a distance from pig sties have averted new Nipah virus spillover from bats to pigs.³¹⁶ In Bangladesh, Nipah virus spillover from bats to humans through drinking uncooked date palm sap infected with bat saliva and urine can be prevented by covering clay pots with bamboo skirts overnight.³¹⁷ In live-bird markets, avian influenza outbreaks and viral genome reassortment can be minimised by limiting poultry population size and stay-time.³¹¹

Large-scale natural habitat restoration and reforestation programmes, which are mostly undertaken to pursue carbon sequestration³¹⁸ and biodiversity conservation goals, could also be harnessed as a form of physical distancing that reduces the risk of wildlife-origin disease transmission by drawing reservoir wild animal populations away from livestock farms and human settlements.³¹⁹ However, reforestation interventions require careful planning, as in some circumstances they may actually contribute to the risk of infectious disease emergence or range expansion. In the US and parts of Europe, for example, over the past

two decades, a combination of reforestation of farmland, rebounding of deer populations and warmer temperatures is believed to have caused a range expansion of the deer tick (*Ixodes scapularis*) and the Lyme disease of which it is a vector.³²⁰ Moreover, planting trees in discontinuous land patches rather than to connect forest fragments, as well as planting monocultures within forest fragments, may have the effect of contributing to rather than decreasing forest fragmentation.¹¹³

Logging, mining, cash crop, ranching and infrastructure construction companies should be legally required to include zoonotic spillover risk reduction measures in their management plans. These measures would include minimising natural habitat fragmentation, adopting wild animal physical distancing measures, providing worker camps and emerging settlements with access to affordable and sustainably produced legume, fish and farm-reared animal protein, monitoring and sanctioning illegal wild meat hunting, sale and transportation at their sites, and promoting biosecurity measures among indigenous communities that practice legal hunting.^{106,299}

Furthermore, interventions exist that target wild animal reservoirs and vectors, such as vaccination, culling and vector management. Owing to differences in reservoir and vector species ecologies, no strategy is likely to effectively tackle all wildlife-origin disease transmission pathways.⁸⁴ For instance, while vaccination of domestic and wild carnivores has enabled the eradication of terrestrial rabies in most EU member states,³²¹ it is not as effective against rapidly evolving strains of avian influenza.³²² Culling can sometimes unintentionally enhance pathogen prevalence in the reservoir population by altering movement dynamics (as it may be the case with vampire bats culled to control rabies)³²³ or by reducing herd immunity (as observed with sick bison culled to control brucellosis).³²⁴ Integrated vector management (IVM) strategies that prioritize environmental management, biological control and personal protection over chemical interventions can yield long-term benefits while minimizing negative impacts on ecosystems and public health. However, countries in sub-Saharan Africa face significant human resource and infrastructure challenges to the deployment of IVM.³²⁵

The reintroduction and protection of natural predator and scavenger species has been proposed as an alternative to culling that controls wildlife-borne infectious diseases by reducing the reservoir population size, killing sick individuals and hastening consumption of infected carcasses.^{84,326} On rangelands, for instance, populations of vultures can significantly reduce the risk of bovine tuberculosis, anthrax and other pathogen spillover from uneaten carcasses.³²⁷ In Spain, wolf predation has been shown to reduce

tuberculosis prevalence in wild boar without reducing its population density, as predation-induced mortality is compensated by a reduction in disease-induced mortality.³²⁸ However, in parts of the US, wolf reintroduction to control chronic wasting disease spillover from elks has met with resistance due to potential economic losses that may be caused by wolf predation on livestock, and the interest of sport hunter groups in maintaining large game populations.⁸⁴

Overall, theoretical models of spillover prevention indicate that implementing biosecurity and physical distancing at the wildlife—human interface is a more effective strategy than targeting wild and domestic animals through veterinary treatment or culling. As such, biosecurity and physical distancing strategies constitute an investment priority, in concert with traditional public health measures targeting the human population such as surveillance for case detection, treatment and vaccination.^{84,329} Moreover, while international safety standards for food production and trade exist, such as the Hazard Analysis Critical Control Point (HACCP) standards and the Codex Alimentarius and OIE codes, these are insufficient by themselves to address zoonotic spillover risk occurring ‘upstream’ in the food supply chain. Instead, tackling zoonotic spillover risk requires interventions that target biosecurity, the physical environment and wild animal reservoirs directly at the wildlife—human interface.

Finally, a One Health approach has been endorsed by the WHO, FAO and OIE, based on recognition that human and animal health are interlinked and bound to the health of ecosystems.³³⁰ By integrating medical, veterinary, epidemiological, wildlife ecology, environmental and social science expertise, One Health aims at strengthening countries’ biosecurity and disease surveillance capacity. However, many zoonotic and vector-borne disease control programmes remain focused uniquely on targeting humans (e.g. through vaccination and drug treatment), lacking robust empirical knowledge of the underlying ecological and socio-cultural factors that lead to animal—human disease transmission. This is particularly true of neglected infectious diseases that primarily affect marginalised populations in low-income countries (e.g. leishmaniasis, leprosy, hydatidosis).^{84,306}

Conclusions

The extensive literature examined in this Review highlights how the potentially increasing incidence of human infectious diseases originating in wild animals may be yet another sign of the way in which the current trajectory of ecosystem degradation is undermining the capacity of planet Earth to sustain human

wellbeing. Considering the enormous health and socio-economic costs of wildlife-origin infectious disease epidemics and pandemics, preventing agricultural encroachment and over-harvesting of wild animals in the last remaining wildlands constitutes an important precautionary strategy to reduce such public health risk.

This strategy implies a global transition towards predominantly plant-based diets that are both healthier and more environmentally sustainable, and drastic reductions in tropical urban wild meat demand. Such actions are also key to the pressing need of mitigating global warming and biodiversity loss, and of safeguarding vulnerable farmer, pastoralist and hunter-gatherer communities who live in marginal landscapes and are strongly reliant on a stable climate and wildlife populations for food and income security. As such, tropical livestock-driven deforestation and urban-driven wild meat over-harvesting have become key issues in the multiple global agendas of environmental conservation, rural poverty relief and, pending further research, zoonotic infectious disease prevention.

Fifteen years of warnings from epidemiologists of the devastating consequences of increasing zoonotic disease risk have been ignored.^{25,331} Likewise, government responses to unprecedented global warming and wild species extinction crises have been inadequate and inconsistent.^{332,333} Yet, as a sustainable global future depends on urgent transformative change of current socio-cultural systems, there is no substitute for early action.^{196,334} It is to be hoped that the COVID-19 crisis will act as a trigger for global societies to recommit to what is most vital, prompting them to examine and act upon the scale of environmental disruption and the threat of zoonotic disease that we are facing. Part of recovery funding should be strategically allocated to implementing research and policies to promote radical shifts in human diets away from heavy reliance on livestock source foods and drastic reductions in tropical urban wild meat demand. This is crucial to simultaneously protect the environment, prevent the exacerbation of rural poverty and reduce the risk of a next zoonotic pandemic.

Contributors

Giulia I. Wegner is responsible for the conceptualisation of this scholarly Review paper (i.e. for the formulation and evolution of its overarching research goals and aims), for its overall design, and for writing the initial draft. She is also responsible for leadership and

coordination of contributions by other co-authors, the illustrator and the photographer.

Kris A. Murray and David M. Morens contributed to the evolution of the aims of the paper.

Kris A. Murray, Marco Springmann, Adrian Muller, Susanne H. Sokolow, Karen Saylor and David M. Morens contributed to writing the final draft through critical review and commentary.

Emily Wright is responsible for the creation of all graphic illustrations.¹

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Supplementary materials

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