Title: Impacts of anthropogenic change on biodiversity affect disease spillover risk

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Summary

The integration of biodiversity conservation and public health has gained significant traction, leading to new efforts to identify win–win solutions for the environment and health. At the forefront of these efforts is pin-pointing ways in which biodiversity conservation can reduce risk of zoonotic spillover, especially given the consequences of epidemics and pandemics of wild animal origin. However, there is currently an incomplete understanding of the mechanisms by which biodiversity change influences the spillover process, limiting the application of integrated strategies aimed at achieving positive outcomes for both conservation and disease management. Here, we review the literature, considering a broad scope of biodiversity dimensions, to identify cases where zoonotic pathogen spillover is mechanistically linked to changes in biodiversity. By reframing the discussion of biodiversity and disease using mechanistic evidence while encompassing multiple aspects of biodiversity, including functional diversity, landscape diversity, phenological diversity, and interaction diversity, we work toward general principles that can guide future research and more effectively integrate the related goals of biodiversity conservation and spillover prevention. We conclude by summarizing how these principles could be used to integrate spillover prevention into ongoing biodiversity conservation initiatives.

Introduction

The COVID-19 pandemic has brought the threat of zoonoses to the forefront, creating widespread demand for managing ecological sources of disease spillover and emergence. Prior to this pandemic, increasing recognition of the ties between healthy ecosystems and human health were beginning to garner support of global conservation initiatives and spurred the United Nations' (UN) adoption of sustainable development goals (the 2030 Agenda). Zoonotic spillover prevention is a biosecurity imperative with a patent connection to the human–wildlife interface; thus, efforts are underway to identify win–win solutions for biodiversity conservation and zoonotic disease management[1]. However, given the incomplete understanding of the mechanisms linking biodiversity to infectious disease spillover, a clear vision of efficacy and pathways for win–win solutions for health and the environment is needed. Increased attention to, and resources for, zoonotic disease prevention make it an opportune time to study the mechanisms connecting changes in biodiversity with zoonotic disease spillover, and to identify (potentially synergistic) solutions for biodiversity conservation and global health.

The discussion around biodiversity and disease has led to a contentious debate about the existence and generality of a biodiversity–disease relationship: in particular, the extent to which maintaining biodiversity protects against disease via a dilution effect, and the alternative possibility that biodiversity can increase infectious disease transmission via an amplification effect (e.g., [2–9]). With a few notable exceptions[10–16], this debate has largely focused on correlations between host species richness and reservoir host pathogen prevalence. However, this narrow framing of impacts of species richness on host prevalence in most of the empirical literature provides limited insight into the range of mechanisms by which biodiversity affects disease, rendering it difficult to integrate into public health interventions. Here, we expand the focus to the broader mechanistic relationships among a variety of components of biodiversity and the zoonotic spillover process, followed by a review of general principles with applied relevance. Finally, we highlight opportunities where ongoing conservation initiatives could consider these mechanisms further in order to reduce disease spillover risks (Table 1, Table 2, Figure 1).

Biodiversity encompasses all forms of variability among living organisms and the ecological complexes of which they are a part; these different forms of variability have long been studied and summarized into related but alternative definitions of biodiversity by other ecological fields[17] (Box 1). Change in taxonomic diversity, including species richness, is often an observable outcome of changes in other types of biodiversity that more explicitly guide conservation efforts such as the loss of functional groups, changes in interaction networks, and heterogeneity in habitat composition. Identifying how these underlying axes drive proximate changes in ecosystem processes like disease transmission, is critical for responding to anthropogenic change[10–16]. Biodiversity can mechanistically affect spillover through several pathways as zoonotic spillover is influenced by many ecological processes before a pathogen actually spills over into a human host, including reservoir host density, distribution, susceptibility, and pathogen prevalence, infectiousness, survival, dissemination, and host–human contact[18,19] (Figure 1). Once in the recipient (human) host, a series of biological and epidemiological factors determine whether onward transmission is possible[18–21] (Figure 1). To harmonize spillover prevention and biodiversity conservation, a clear mechanistic understanding is needed of how increases and decreases in multiple aspects of biodiversity, from individuals to populations to communities to ecosystems, influence various spillover processes (Figure 1).

This review focuses on how infectious disease systems change with shifts in biodiversity, highlighting case studies that suggest causal mechanisms (Table 1, Figure 1). We group case studies based on the leading International Union for Conservation of Nature (IUCN)-classified threats to biodiversity. While examples that mechanistically link environmental change to zoonotic spillover via at least one metric of biodiversity change are scarce, our review identifies emerging generalities across disease systems and anthropogenic disturbances. We find the best support for an influence of functional, interaction, ecosystem phenological, and landscape diversity on spillover risk but recognize that there are additional dimensions of biodiversity not explicitly studied that are likely to influence spillover (e.g., genetic diversity[22]). Within our description of the generalities, we identify ongoing sustainability initiatives that could incorporate spillover prevention, emphasizing how reframing the discussion about biodiversity and disease may facilitate win–win outcomes for health and the environment.

Anthropogenic disturbance, biodiversity change, and disease spillover

Land conversion, agricultural intensification, and urbanization

As of 2019, agricultural expansion and intensification were the leading causes of biodiversity loss[17]. Agricultural development fragments and clears previously intact ecosystems, creating edge habitats that increase human encroachment on wildlife, homogenizing landscapes to reduce availability of natural resources for wildlife, and releasing pesticides, fertilizers, and antimicrobial compounds into the environment. Urbanization, characterized by built environments, similarly clears intact ecosystems while increasing air, water, light, and land pollution[23]. Moreover, urbanization significantly increases human density: 70% of the world's population are expected to live in urban areas by 2050[24]. All of these factors contribute to population declines or even local extinctions of species[25–27] and may influence the dynamics of infectious diseases with an important environmental component in their transmission cycle[28].

Clearing intact ecosystems for agriculture, urbanization, and other land modifications (including development of forestry), drive the loss of large- and medium-bodied animals (i.e., defaunation) while supporting the persistence or growth of populations of small-bodied animals[29–32]. Recent research has made it clear that loss of functional diversity (defined in Box 1) due to non-random patterns of defaunation has significant effects on zoonotic spillover risk[10,11,16,33–39]. Increase in disease spillover risk due to changes in functional diversity of animal communities may occur through expansion or invasion of opportunistic zoonotic hosts that thrive in human modified landscapes or through the cascading effect of human-induced extirpation of predators and competitors of zoonotic species, as described below.

Small-bodied mammals are common pathogen reservoirs, with the rodent and bat orders containing the highest number of known zoonotic hosts[40–43]. Certain taxa of small-bodied animals are likely to predominate in human-modified landscapes due to traits that make them adaptable to living in proximity to humans[44,45]. These traits, including diet and habitat generalism with fast-paced life history, high population density and proximity with human settlements, are positively correlated with zoonotic reservoir status[12,34,41]. On a global scale, the richness and abundance of zoonotic hosts (especially birds, bats, and rodents) positively correlate with degree of human land modification[34,46]. Local studies in Kenya, Tanzania, and Madagascar found that this change in functional diversity, so that communities are dominated by animals with traits conducive to adaptation to human environments, increases zoonotic disease risk: rodent communities in croplands had a higher proportion of competent zoonotic reservoir hosts and higher prevalence of zoonotic pathogens than in unmanaged areas[16,35,47].

Loss of functional diversity of ecological communities may be driven also by the loss predators and competitors that help regulate populations of reservoirs hosts and vectors. Land conversion can drive the replacement of large herbivores with small herbivores, altering the overall effect of herbivores on the plant community and ecosystem as a whole[33,48]. In savanna ecosystems in Central Kenya, exclusion of large herbivores through fencing, an experimental simulation of what often occurs with agricultural intensification, resulted in changes in the plant community and competitive release of small herbivores, leading to the increase in abundance of competent rodent hosts (*Saccostomus mearnsei*) and prevalence of *Bartonella* and vectors[33,49] (Table 1, Figure 1). Predators of reservoir hosts and vectors might also exert a crucial role in modulating the risk of disease spillover for humans[10,11]. In Senegal, the construction of the Diama dam in 1986 to prevent saltwater intrusion and support agriculture intensification blocked the migration of native predators (the giant river prawn, *Macrobrachium vollenhoveni*) that consume snail vectors and free-living *Schistosoma* spp., resulting in increased transmission of vector-borne parasites to humans[36]—these findings have been linked to construction of large dams and subsequent increases in schistosomiasis transmission throughout Africa[38]. In terrestrial zoonotic disease systems, the presence of leopards may decrease risk of rabies transmission to humans by preying on stray dogs in Mumbai, India[37]. Further, predator loss can trigger significantly more complex trophic cascades. The loss of wolves in the Northeastern USA was followed up by an increase in coyotes, which in turn led to a dramatic reduction of predators of small-mammals that control the abundance of rodents competent hosts for Lyme disease[11]. This release of competent rodent reservoir hosts from predation has been linked to expansions in Lyme disease in the last two decades[10,11].

In general, land conversion for agriculture can affect landscape diversity (Box 1), thereby altering species distributions and changing contact patterns between wildlife and humans[50–52]. Landscape diversity can be described as compositional diversity, including patch type diversity, and configuration diversity, including number, size, and arrangement of patches. These aspects of landscape diversity have nonlinear and complex responses to anthropogenic change[53]. As many existing biodiversity initiatives center around land conservation and restoration, including landscape diversity in the biodiversity–disease discussion is crucial for identifying synergistic solutions for biodiversity conservation and preventing zoonotic spillover. Within monocultures, all metrics of landscape diversity are reduced. However, in relation to intact ecosystems moderate agricultural conversion has various effects on patch type diversity, decreases patch size and thus variation in patch size, and increases the distance among intact habitat patches[54–56]. Fragmenting of habitat into small patches can shift the distribution of reservoir species to aggregate at high densities near humans, increasing contacts between humans, previously unencountered mammals, and vectors, thereby increasing potential for transmission[57]. For example, *Plasmodium knowlesi* malaria is expanding in Malaysia and across Southeast Asia, partially due to forest loss and agricultural land conversion[58–63], which drives the primary reservoir hosts, long-tailed macaques

(*Macaca fascicularis*) and pig-tailed macaques (*Macaca nemestrina*), to occupy small forest fragments within or next to agricultural areas where they overlap with anthropophilic mosquito vectors and people[63–65]. This shift in distribution not only increases the density of reservoirs, potentially increasing transmission among reservoir hosts, but also increases potential for macaque–vector–human transmission[63] (Table 1). High profile zoonotic pathogens, such as Ebola virus, similarly spill over in forest fragments[66,67], highlighting the links between changes in landscape configuration and diversity on zoonotic spillover risk.

Shifts in landscape diversity that skew functional diversity towards favoring reservoir hosts may additionally increase the risk of antimicrobial resistant (AMR) zoonotic spillover. Runoff from antibiotic-fed livestock forms wastewater lagoons where diverse bacteria mix and face strong selective pressures to develop and share, via horizontal gene transfer (HGT), genes conferring resistances to those antibiotics[68,69]. This also occurs in aquacultural waters[70], wastewater from antibiotic-treated crops[71], and effluent from wastewater treatment plants[72]. Wildlife that contact polluted waters or soils can pick up these AMR bacteria and transport them to both neighboring and distant croplands or livestock operations where they can spill over to people[73–77]. Global rates of AMR are on the rise, driven by the misuse of antibiotics in clinical settings as well as in agriculture, with an estimated 700,000 deaths worldwide caused by AMR bacterial infections[78]. While research efforts on wild animal reservoirs of AMR bacteria are severely limited[79], initial research shows that animal populations proximate or adaptable to human modified habitats have higher prevalence of AMR bacteria than animals with little to no contact with humans[80], perhaps due to higher host competency and/or exposure rates to these potentially infectious agents. Smith et al.[80] found that the prevalence of AMR bacteria in agricultural areas decreased as the amount of native habitat increased, possibly due to reducing contact rates of birds with livestock runoff. As a result, landscape composition and configuration may reduce the likelihood of birds becoming inoculated with and transmitting AMR bacteria. Landscape diversity may jointly decrease AMR risk by protecting croplands from livestock wastewater runoff and by providing vegetation that acts as natural ecosystem filters[81]. The effect of biodiversity change on AMR spillover is severely understudied but, given the threat of AMR bacteria to global public health[82], warrants significant attention[79,80].

Further, land conversion can reduce the phenological diversity of natural ecosystems and food sources (i.e., ecosystem phenological diversity, defined in Box 1), which can cause nomadic and migrating species to forgo migration in favor of occupying the same habitat year-round. In some cases, formation of resident populations may shift reservoir host dynamics to alter zoonotic spillover risk, particularly when loss of seasonal, high-quality natural resources is paired with provisioning of non-seasonal, subpar food[83]. For example, loss of optimal winter resources, at least in part due to habitat loss, drives reservoir hosts (*Pteropus* spp.) of Hendra virus from large nomadic groups that track seasonally abundant nectar sources into small resident groups feeding on permanent, suboptimal food within and around cities[21,84,85]. Food stress may promote viral shedding; simultaneously, the redistribution of reservoir hosts into smaller yet more abundant colonies in human-dominated systems increases the likelihood of the virus spilling into amplifying hosts (i.e., hosts in which a pathogen can rapidly replicate to high concentrations, for example horses in this case) and humans[86]. Similarly, agricultural conversion has limited the availability of high-quality winter resources for elk. Large populations are now supported by lower-quality supplemental feeding, which reduces migration and promotes high density aggregations, thereby increasing the spread of *Brucella abortus* among reservoir hosts and potentially spillover to livestock[87–90]. Climate change may further exacerbate loss of phenological diversity and interrelated shifts in animal movement, however, this has not been explicitly linked to zoonotic spillover[91].

Finally, the rural to urban transition diversifies local economies from dependence on local agriculture to trade of goods, services, and ideas with more distant places[92] . Through trade with rural areas, urbanization interacts with other threats to biodiversity, such as introduction of pathogens through the wildlife trade and introduction of invasive species, to drive changes in zoonotic spillover[93]. Drastic reduction of non-human adapted animals in completely converted land (i.e., cities) may reduce the frequency of spillover of novel zoonotic pathogens[94]. At the same time, interactions between urbanization and other anthropogenic disturbances creates circumstances for pathogen introduction, especially if pathogens can be sustained via human–human transmission. For example, urban centers serve as hubs for long-distance shipping, with urban wildlife markets often containing higher densities and diversity of wildlife. Thus, urban wildlife markets create unique assemblages of species subsequently increasing the likelihood of novel cross-species transmission[95]. Then, in the rare case where the biology of the pathogen allows frequent human–human transmission (e.g., high infectivity to humans, asymptomatic transmission, aerosol transmission[19]), the large and dense human population found in cities can facilitate rapid pathogen spread, resulting in the largest epidemics[94] or even pandemics. Spread of novel zoonotic pathogens may be mitigated by increased health and subsequent reduced susceptibility in affluent urban[96]. However, the opposite may be true in unplanned urban areas or urban areas designed to oppress groups of people (i.e., without centralized infrastructure and equitable distribution of resources) where human health might be compromised by increased pollution, lack of affordable healthcare, and limited access to healthy food and clean water[93,97].

Climate change

Species may respond to climate change through plasticity[98], rapid adaptive evolution[99], and altitudinal and latitudinal range shifts to the edge of their geographic range[100–102]. Alternatively, species may undergo local population extinctions, range shifts, or even global extinction[103–107]. Further, the velocity of rising temperatures differs among regions of the world, affecting species and populations differently[108]. Together these responses can drive biodiversity change in complex, nonlinear, and interdependent ways. Here, we focus on case studies of range shifts in response to rapid anthropogenic climate change, as it is the most immediately observable impact of climate change on wildlife hosts harboring zoonotic pathogens[109,110]. Plastic, adaptive, and local declines or extirpation responses are currently well researched[111–113], with the amphibian decline being perhaps the most emblematic case[114], but they are rarely connected to pathogen spillover.

The abundance of different species with certain traits or ecosystem functions (e.g., diet, habitat, activity patterns, etc.), and thus functional diversity, may decline with range shifts, especially at high latitudes, although taxonomic diversity (Box 1) of some systems may increase with range shifts[115–117]. This is largely attributed to generalists outnumbering specialists in systems impacted by global change, as generalists are able to thrive in a variety of ecological conditions, including human modified landscapes, while specialists need specific resources and/or habitats to survive. At the same time, correlative analyses suggest that zoonotic reservoirs are more likely to be generalist species[34,39,118], as they are more likely to live in closer proximity to people and contact a wider range of other host species. Further, climate-induced forest habitat loss may lead to an increase in abundance of extreme generalists with zoonotic reservoir potential, as in the case of the highly adaptable deer mice harboring Sin Nombre virus[119].

The Alaskan Arctic is currently exhibiting climate-induced shifts in host species, with an increase in the abundance of zoonotic hosts more likely to contact humans. Before contemporary climate change, the ranges of two carnivores and rabies reservoir hosts, red and Arctic foxes, were separated[120]; however, with climate change the home range of the generalist red fox has expanded northward, encroaching on the territory of the comparatively habitat-specialist Arctic fox[121]. Arctic fox numbers were already in decline due to other effects of climate change, such as the loss of sea ice and tundra habitat as well as loss of lemming prey, but red foxes are expediting this decline through intraguild predation and competition for resources[122–124]. As Arctic fox populations are replaced by red fox populations, the red fox will become the primary reservoir for rabies spillover. This shift in the reservoir community will likely increase epizootic peaks of rabies as immigrant red foxes interact more with resident Arctic foxes, increasing both the transmission rate and the overall density of susceptible individuals[125]. Further, because the larger-bodied red fox displays more aggressive behavior than the Arctic fox[120], and because it is more amenable to adapt to human-dominated landscapes, contact rates between wild rabies reservoirs and dogs or humans might increase, thus increasing rabies spillover risk (Table 1, Figure 1).

Climate change may reduce other dimensions of biodiversity beyond functional diversity. For instance, climate change may reduce landscape diversity by reducing patch diversity and subsequently increase the likelihood of cross-species transmission through increased habitat overlap and taxonomic diversity in confined areas[126]. For instance, the melting of sea ice alters, disrupts, or even prevents migration patterns of animals such as wild caribou[127], increasing the chance of intermingling among caribou and other wild or domestic ungulates. Thus, people who rely on caribou and/or other livestock might be at higher risk of brucellosis spillover under a warming climate in temperate regions[128]. Similarly, in water-stressed parts of Africa, extreme droughts can force many animals that previously used different water bodies and had little to no contact with one another (such as humans, wildlife, and livestock) to congregate at common water sources[129,130], increasing traffic and reducing water quality due to elevated fecal loads. In Chobe National Park, Botswana, these patterns and processes are associated with increased loads of *E. coli*, the leading cause of diarrheal outbreaks[130]. Following drought events in and around Chobe National Park, heavy seasonal rainfall and flooding mobilize pathogen-containing feces, subsequently leading to human diarrheal outbreaks in neighboring communities[131] (Table 1). Further, these water sources have potential to serve as melting pots of antimicrobial resistant bacteria and sources of novel pathogen emergence[132].

Invasive species

Invasive species (i.e., organisms that establish and spread outside their native range) negatively impact native biodiversity, ecosystem services, or human wellbeing, presenting a significant threat to ecosystems[133]. Through processes such as predation, competition, or environmental modification, invasive species can drastically decrease the biodiversity of an ecosystem; an estimated thirty species of invasive predators alone are responsible for at least 58% of all bird, mammal, and reptile extinctions globally[134]. Invasive species can indirectly impact infectious disease by altering the structure and composition of the native community in ways that either increase or decrease pathogen transmission.

Altering a native community to increase zoonotic spillover risk has been empirically demonstrated for the Everglade virus, a mosquito-borne zoonotic virus. The introduction of the Burmese python (*Python bivittatus*) to the Florida Everglades has led to large-scale declines in functional and taxonomic mammal diversity due to precipitous loss of large and small-bodied mammals[135,136]. With loss of mosquito food sources due to python predation on deer, racoons, and opossums, mosquito vectors of Everglades virus fed dramatically more on the primary reservoir host of the virus, the hispid cotton rat (*Sigmodon hispidus*), resulting in higher rates of Everglade virus infection in mosquitoes, and potentially increasing the risk of virus exposure to humans[136,137]. The Burmese python–Everglade virus case study is a clear example of the dilution effect (i.e., higher taxonomic diversity of hosts reduces disease risk and the loss of that diversity increases disease spillover risk), which can readily occur for vector-borne, zoonotic pathogens for which the vector can take “wasted bites” (from a pathogen transmission perspective) on non-competent hosts, as is the case here[9].

In contrast, introduction of invasive species can reduce transmission of infectious disease from vectors to people through predation on various vector life stages (larvivorous fish on malaria vectors[138]; crayfish on schistosome intermediate hosts[139]). However, despite crayfish lowering the risk of schistosomiasis by voraciously consuming snail intermediate hosts and free-living parasites, invasive crayfish compromised other dimensions of human health by consuming rice and degrading canal banks with their burrows[140]. Consequently, in scenarios where invasive species reduce disease risk there can still be a tension between biodiversity impacts of invasive species and their specific ecological roles in infectious disease dynamics.

Invasive species may affect infectious disease dynamics by acting as vectors or reservoir hosts[40,47,141–143], sharing pathogens with native species[144–146], or providing resources for reservoirs and/or vectors[143,147]. In these cases, biodiversity conservation via invasive species control may simultaneously reduce zoonotic spillover risk[143]. The same processes that drive species introductions, including global trade and travel, may also drive disease emergence, suggesting that win–win solutions for protecting ecosystems from species invasion and humans from pathogen spillover might be possible, though potentially technically and politically challenging[148].

Wildlife hunting, trade, and consumption

One in five vertebrate species is impacted by trade[149], with some wildlife facing population declines and/or species extinction due, mainly or in part, to the impacts of legal and primarily illegal wildlife trade (e.g., tigers, rhinoceroses, elephants, sharks, and pangolins)[150,151]. The illegal wildlife trade is estimated to be the world’s second largest underground businesses (hypothesized to be a $5–20 billion-dollar industry) after narcotics[152]. The legal wildlife trade, estimated to be an even larger business ($300 billion-dollar industry), also poses a threat to biodiversity as the majority of legal wildlife trade (78%) is composed of wild caught animals, as opposed to those reared in captivity[153]. The local increase or decrease of biodiversity, as well as novel contacts between species that do not co-occur in the wild, as different species are being translocated via trade may drive spillover and disease emergence, as explained below.

Epidemiological and genetic analyses have linked wildlife hunting, trade, and consumption to spillover and spread of many high-profile zoonotic pathogens: rabies virus, Crimean-Congo hemorrhagic fever virus, the plague-causing bacteria *Yersinia pestis*, monkeypox virus, coronaviruses, HIV, Marburg and Ebola viruses[150,151,153–156]. However, in order to stop or mitigate the spillover process, we need to better understand the mechanisms linking the wildlife trade to the eco-epidemiological process of spillover (Figure 1).

The wildlife trade highlights how anthropogenic pressures can increase spillover risk via a direct increase in both taxonomic diversity and the number of interactions across taxa (i.e., interaction diversity, defined in Box 1) on very small spatial scales. Throughout the supply chain, the wildlife trade brings together high densities of species that typically would not contact each other in natural habitats. These unique assemblages and interactions can promote cross-species transmission, increasing the likelihood that a pathogen may be transmitted to amplifying hosts and/or humans[154,157–163]. Trade may also impact the spillover process by promoting pathogen shedding from animals because of unsanitary conditions during, and stress from, transportation and market[154,157–163]. For example, the ancestor to SARS-CoV-1 is suspected to have been transmitted from horseshoe bats (most likely *Rhinolophus sinicus*) to palm civets, two species that do not interact in wild settings. However, palm civets served as amplifying hosts or as intermediate hosts within wildlife markets, bringing the virus in closer proximity to humans[164–166]. Seroprevalence and virological testing surveys of civets on farms *versus* those brought to markets in Guangdong, China suggest that palm civets were exposed to the virus at the end of the supply chain[165–167]. A study performed in Vietnam showed that coronavirus detection in field rats caught or reared for human consumption more than doubled when testing field rats sold in markets, and further increased by 10-fold when testing field rats sold or served in restaurants, compared with rats in the wild[162]. Thus, the wildlife trade creates opportunities for increased transmission among multiple wild animal species and puts humans in closer proximity to stressed and infected wildlife, fueling the potential for spillover of pathogens (Table 1, Figure 1).

The wildlife trade for human consumption can take on various forms, including commercial harvesting of wild animals on land and at sea, which in turn can interact to amplify the effects of overharvesting, leading to a decrease of many types of biodiversity, such as taxonomic, genetic, functional, interaction, and landscape diversity (Box 1). For example, the wild meat trade in Ghana, which has driven population declines of some mammalian species in the last few decades, correlates with local declines in fish supply, probably due to commercial overfishing off the coast[168,169]. Conceivably, during periods when the demand for wild meat is high, hunters and people involved with the butchering and preparation of the meat expose themselves to a higher risk of disease spillover from bites, scratches, and other contacts with bodily fluids of animals serving as reservoirs for many pathogens. In the Congo basin and other regions where pathogens have recently emerged, wild meat serves as a protein source primarily in impoverished households, making the banning of wild meat a controversial topic[170], though genetic and epidemiological evidence suggests that it has contributed to the rise of emerging diseases and recent outbreaks via spillover from wildlife to humans of pathogens like Ebola (Table 1), HIV, Marburg, and monkeypox viruses[154,171,172]. In Cameroon, simian foamy viruses regularly spill over and infect wild meat hunters, but no human–human transmission has yet been established[154]. Conversely, HIV has adapted to undergo human–human transmission, but phylogenetic analyses suggest that approximately 10 spillover events occurred over the past century before HIV caused a pandemic, suggesting that frequent spillover during bushmeat hunting was critical for its emergence as a pandemic[151].

Overexploitation of wild meat and other anthropogenic pressures have also been correlated with a decrease in the proportion of large-bodied mammals and an increase in the proportion of small-bodied mammals brought to market[173,174]. As a result, preliminary research suggests that overharvesting of wildlife may influence the types of wild animals hunters and consumers are contacting, potentially presenting new zoonotic spillover risks; however, mechanistic links between change in composition of wildlife markets and zoonotic disease risk have not yet been established.

Incorporating concepts of ecological diversity to mitigate spillover risk

While mechanistic research linking changes in biodiversity to zoonotic spillover risk is limited due to the expense and logistical challenges of elucidating these relationships, by considering more mechanism-based changes in biodiversity than species richness and composition, we collect enough empirical examples to propose four general concepts that have potential to inform biodiversity conservation. These generalities may motivate further integration of biodiversity and zoonotic pathogen spillover research, potentially opening more avenues of funding as well as incorporation of multi-disciplinary methods for collecting and analyzing data. To illustrate this application of our synthesis, we identify ongoing biodiversity and sustainability initiatives that could use these generalities to incorporate spillover prevention (e.g., to avoid unintended harms from biodiversity conservation or to broaden the benefits of biodiversity conservation). Echoing Halsey[8], we distinguish between *generality*, that which is mostly considered true, and *universality*, that which is considered true in all possible contexts. These four generalities (described below) may be more or less applicable for different ecosystems and disease threats.

First, loss of spatially and phenologically diverse habitat alters the spatio-temporal distributions of reservoirs, leading to increased overlap with other vertebrate hosts, vectors, and humans. This generality suggests an opportunity: preserving and restoring large, contiguous, and heterogeneous habitats could minimize harmful contact between humans and wildlife and between host species that do not commonly interact (e.g., a reservoir and an amplifying host) while additionally reducing the density of reservoir hosts and subsequent intraspecific contact and transmission. The Bonn Challenge[175], Thirty-by-Thirty Resolution to Save Nature[176,177], Payments for Ecosystem Services[178–180], and Project Finance for Permanence projects[181–183] all include conservation and/or restoration of natural ecosystems but do not incorporate spillover prevention in project design and implementation (Table 2). Intact and diverse contiguous landscapes may also promote landscape immunity, defined as ecological conditions that maintain and strengthen the immune system of wild animals to reduce pathogen susceptibility and shedding, particularly for potential reservoir species including bats and rodents[184,185]. Further, targeted habitat conservation and restoration could encourage previous migration patterns by re-creating or maintaining phenological diversity of high-quality food sources, such as nectar resources for bats[21,143]. However, in some cases, resource provisioning—through invasive species, crops, and even waste disposal practices—may reduce migration even when endemic, phenologically diverse habitats are available[186,187]. More research differentiating the impact of habitat restoration *versus* limiting human provisions (e.g., through clearing of invasive plants or better waste disposal management) is needed. Importantly, some biodiversity conservation initiatives such as Payment for Ecosystem services in Costa Rica[179] include agroforestry, which could hypothetically increase human exposure risk to zoonotic disease[188]. In these cases, the effect of landscape diversity and specific agroforestry practices on spillover should be considered so as not to put biodiversity conservation and public health at odds. Overall, studying the mechanistic effect of landscape diversity and ecosystem phenological diversity on each spillover process (Figure 1) should lead to new insights that can guide evidence-based policy for both conserving natural ecosystems and reducing spillover risk.

Second, loss of large consumers and predators (changes in functional diversity) can result in increased abundance of animals with fast growth rates and relatively small ranges, such as rodent reservoirs and arthropod vectors. Regulation of poaching (e.g., via the Convention on International Trade in Endangered Species[189] initiative), and habitat conservation, preservation, and restoration of contiguous, intact ecosystems could support populations of large predators and herbivores[174,190,191]. In turn, predators and large consumers may be important in ecotones between intact and anthropogenic landscapes, where they can regulate populations of small-bodied reservoirs that thrive in human modified areas. The initiatives aimed to restore and conserve habitat in Table 2 could be adapted to support populations of wildlife that help regulate rodent populations. For example, the Thirty-by-Thirty Resolution to Save Nature[176,177] proposes conservation of wildlife habitat and corridors for safe passage of wildlife between intact habitats—this plan could be improved by configuring habitats and corridors to best support populations of keystone predators and large consumers in areas of zoonotic disease risk. More research is needed to understand the impacts large herbivores and predators have on zoonotic disease regulation, especially within and around ecotones. If more evidence supports a beneficial effect of conserving predators and large herbivores for reducing spillover risk without increasing human–wildlife conflict, conservation of predators and large consumers may offer another promising win–win situation for environmental and human health.

Third, human modification further affects functional diversity by changing habitats and shifting communities toward dominance by species that are resilient to anthropogenic disturbance or thrive in human-dominated landscapes, which are more likely to be zoonotic. Change in functional diversity towards synanthropic species has been observed across taxonomic groups of vertebrates (e.g., rodents, birds, and carnivores). Similar effects have been observed for disease vectors in which generalists thrive in urban areas and have high capacity to transmit pathogens to humans[38,192,193]. Integrative approaches, such as direct management of invasive rodents and vectors or indirect management through preserving intact habitat and mitigating impacts of climate change to reduce range shifts of reservoirs and vectors, are likely necessary[143,194]. Initiatives that guide policy and coordinate action to protect biodiversity from multiple anthropogenic threats, such as the Convention on Biological Diversity (CBD)[195], may be particularly well suited to prevent spillover from these human-adapted reservoirs and vectors. For example, CBD sets global priorities and coordinates global action on invasive species and climate change, providing a platform to jointly manage invasive reservoir hosts and vectors while advocating for climate resilient ecosystems on a world-wide scale.

Fourth, commercial wildlife trade, introduction of invasive species, and transportation of livestock and companion animals are activities that increase interaction diversity, introducing more opportunities for cross-species transmission among different species and increasing the chance of new pathogens emerging that may have zoonotic spillover potential. The Convention on International Trade in Endangered Species[189] aims to control the illegal wildlife trade but does not include objectives that prevent spillover: adopting global regulations on pathogen screening and ethical and sanitary animal husbandry standards in the international wildlife trade could be a natural next step in advancing management of zoonotic spillover. Overall, regulations and initiatives that reduce diversity of novel interspecific interactions should be adjusted to incorporate spillover prevention.

Other international initiatives are currently working towards sustainable solutions for promoting both public health and conservation, such as the UN Sustainable Development Goals[196], Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) Nature's Contributions to People[197], IUCN Global Standards for Nature-Based Solutions[198], Bridge Collaborative[199], Pan American and World Health Organizations (PAHO/WHO) Climate Change and Health[200], Global Health Security Agenda[201], and the collaboration among Food and Agriculture Organization (FAO), World Organisation for Animal Health (OIE), and WHO (FAO-OIE-WHO Collaboration)[202]. The initiatives included in Table 2 have not yet incorporated spillover prevention.

We emphasize that the initiatives described here must only be implemented based upon local context, centered around the needs, demands, and culture of the local people. A number of global restoration and conservation efforts have been critiqued as colonialist and thus detrimental to vulnerable and marginalized groups of people. For example, the Bonn Challenge has been critiqued for foresting historically savannah ecosystems, thereby impacting ecosystem function and rangeland livelihoods[203]. Further, the Payment for Ecosystem services in Costa Rica has been rebuked as not adequately compensating people for the service they provide[204] and Thirty by Thirty has been challenged for disproportionately, negatively impacting Indigenous communities while failing to account for their for their outsized, positive effect on biodiversity . These initiatives may be improved by creating context-dependent management plans that are designed around and implemented by local communities and Indigenous groups. One way to achieve this is through conservation of land via Indigenous Protected Areas (IPAs); while defined differently depending on the country, IPAs generally are large areas of intact ecosystems managed or co-managed by Indigenous groups. More than 46% of national reserves within Australia are IPAs[206], and a small but increasing proportion of protected land in Canada are IPAs (e.g., Thaidene Nëné Indigenous Protected Area, the homeland of the Łutsël K'é Dene First Nation)[207]. The United States and countries with similar Thirty by Thirty goals should and could create similar protected areas. Another successful model is Health in Harmony's programs in Borneo, Madagascar, and Brazil, which start with "radical listening" within rainforest communities to co-develop community-based conservation and health programs that reduce deforestation and provide affordable healthcare access[208].

We additionally emphasize that biodiversity conservation is not a panacea for zoonotic spillover prevention, and many systems are too complex or understudied to prescribe clear links between biodiversity change and spillover risk. For example, highly diverse multi-host, multi-vector systems such as West Nile Virus (WNV), Ross River virus[209,210], leishmaniasis[211], and Chagas disease[212], require more studies to document ecological drivers of reservoir and vector abundances and capacities to transmit disease. Further, reservoir host species that contribute most to transmission may be variable along geographic and land-use gradients[213–218]. Even when conservation-related levers for spillover prevention exist, their impacts should be compared to those of other approaches (including economic and biomedical) and implemented from a community-based, environmental justice perspective. Thus, sustainable solutions for alleviating zoonotic disease burden while conserving biodiversity should be evaluated based on specific knowledge of the socio-ecological context[1].

Conclusions and future directions

We identified mechanistic evidence in the literature that in certain systems anthropogenically-driven biodiversity change increases zoonotic spillover risk. Several common themes emerged. First, the loss of intact habitat increases overlap between reservoirs and other vertebrate hosts, vectors, and humans. Second, loss of large-bodied consumers and predators (defaunation) can result in increased abundance of rodent reservoirs. Third, human-modified landscapes change the functional diversity of species assemblages, increasing the proportion of species that are able to adapt and thrive in anthropogenic environments, and thereby increasing human exposure to zoonotic pathogens. Fourth, other forms of anthropogenic disturbance generated by agriculture and trade of domestic animals and wildlife lead to the introduction of invasive species and increase interaction diversity, facilitating opportunities for cross-species transmission and thus the potential for emergence of novel pathogens with zoonotic spillover potential. Hence, anthropogenic drivers of biodiversity change interact in complex ways, including synergies, and direct and indirect effects. The combined impacts among many different anthropogenic disturbances may exacerbate the effects of biodiversity change on spillover risk.

Certain disease systems are either understudied or too complex to elucidate the effects of biodiversity change on spillover risk. In addition, some components of the spillover process (Figure 1) are better studied than others in the context of the impacts of biodiversity change. Based on our review, the effects of biodiversity change on wildlife host susceptibility, pathogen shedding, and pathogen prevalence in the reservoir for example (three important steps of spillover) are understudied compared to human pathogen exposure (Figure 1). This may arise because wildlife host susceptibility, pathogen shedding and prevalence are difficult to observe[219]. Another possibility could be lack of appreciation for how wildlife health—not just presence or absence—may affect zoonotic spillover risk. When exposed to stress from anthropogenic activities, wildlife hosts may experience suppressed immune systems, rendering them more susceptible to opportunistic infections, more pathogen shedding, and altered behavior that increases their exposure to pathogens[185,220]. Thus, increased pathogen surveillance and health assessment in wildlife may interrogate mechanisms by which environmental stressors affecting wild animal health may lead to changes in the process of disease spillover to people and domestic animals. Finally, there is an urgent need for spatially and temporally replicated field studies incorporating biodiversity change, pathogen dynamics, and wildlife host immunology[184,185] in addition to human health outcomes.

The world is undergoing rapid anthropogenic change with detrimental effects on biodiversity and the health of organisms, including humans. Efforts are underway to combat the impact of anthropogenic disturbances on biodiversity. However, since biodiversity change may affect zoonotic disease spillover through multiple mechanisms, it is imperative that biodiversity conservation efforts also incorporate actions to prevent spillover. Spillover is not only an issue for public health, but also for conservation of threatened wildlife. Here, we argue that reframing discussions of biodiversity and disease around a more inclusive definition of biodiversity, and considering the context of each of the complex social-ecological systems in which the spillover process occurs (Figure 1, Box 1) are essential to highlight mechanistic links between biodiversity and zoonotic spillover. This approach sheds light on how to develop sustainable win–win interventions for health and the environment that prevent zoonotic spillover while protecting biodiversity.

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Declaration of interests

The authors declare no competing interests.

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Glidden *et al.* review mechanisms by which biodiversity change—driven by anthropogenic disturbance on the environment—influences disease spillover risk by considering a suite of biodiversity metrics. Finally, this review summarizes general principles that could be used to integrate spillover prevention into biodiversity conservation initiatives.

Figure legends

Figure 1. The anthropogenic disturbance, biodiversity change, and spillover cascade. To understand mechanisms connecting anthropogenic disturbance with spillover via biodiversity change, it is imperative to investigate how anthropogenic disturbance impacts biodiversity, and how those effects drive the perforation of the layers (intermediate processes) leading to spillover (shown using four case studies from Table 1 as examples). Zoonotic spillover arises from the alignment of multiple processes (depicted as layers). Apart from human susceptibility to infection, we found that each layer can be affected by biodiversity change, especially when considering biodiversity along multiple axes (Box 1). Connecting biodiversity change to explicit processes helps us to better understand how, when, and why biodiversity change impacts zoonotic disease risk. Numbers next to each layer correspond to case studies highlighted in Table 1. All references for these case studies are included in Table 1.

Box

Box 1. Examples of dimensions of biodiversity

Biodiversity is made up of a number of dimensions, with multiple axes affecting zoonotic spillover risk. Below are a handful of biodiversity type examples described by[22], with suggestions for measuring and tracking each type of biodiversity made using the universally developed GEO BON essential biodiversity variables (EBVs)[221]:

● Genetic diversity: Aspects of genomic variability, including nucleotide, allelic, chromosomal, and genotypic. Genetic diversity has yet to be studied in the context of biodiversity change and zoonotic disease risk; however, multiple reviews[14,15] have described how observable patterns in taxonomic diversity are likely, at least in part, the result of genotypic variation governing variation in host physiology and behavior (i.e., host resistance, tolerance, and competence) and thus can influence zoonotic disease risk. EBVs: Intraspecific genetic diversity, Genetic differentiation

● Taxonomic diversity: The number and relative abundance of taxa (e.g., species, genera, and higher levels of taxonomic organization). Disease–diversity relationships are typically described within the context of species richness. Examples relevant to spillover include increase in diversity of host species so that vectors take "wasted bites" on non-competent hosts. In many cases, change in taxonomic diversity *per se* does not influence zoonotic disease spillover; however, change in the other dimensions of biodiversity are evident through change in taxonomic diversity. EBVs: Species distributions, Species abundances, Community abundance, Taxonomic/phylogenetic diversity

● Functional diversity: Variation in the degree of expression of multiple functional traits, i.e., the different types of processes in a community that are important to its structure and dynamic stability. Examples relevant to spillover include loss of predators and competitors and increase in abundance of generalist, synanthropic animals. EBV: Trait diversity

● Interaction diversity: The number and relative abundance of interactions among species in a community[222]. The biotic interactions include contact, competition, facilitation, and predation. Examples relevant to spillover include loss of interactions regulating reservoir host species or by increased number of novel cross-species interactions via crowding. EBV: Interaction diversity

● Ecosystem phenological diversity: Diversity in the phenological dates of life within an ecosystem (e.g., flowering time). A subset of temporal diversity, which is broadly change in biodiversity over time. Examples relevant to spillover include reducing the seasonal availability of resources, in turn affecting sedentary movement and eating habits. EBV: Phenology

● Landscape diversity*: Landscape compositional diversity, including patch type diversity, and configuration diversity, including number, size, and arrangement of patches. Examples relevant to spillover include increasing number of reservoir habitat patches while decreasing their size, thereby providing increased opportunity for host-human or host-vector contact. EBVs: Live cover fraction, Ecosystem distribution

*landscape ecologists commonly refer to landscape diversity as heterogeneity

Tables

Table 1. Case studies of mechanisms connecting anthropogenic disturbance with biodiversity change and its subsequent effects on infectious disease spillover. Figure 1 illustrates the overall framework for linking anthropogenic disturbance to biodiversity change to disease spillover via the spillover layers being affected in each case study.

Anthropogenic disturbance	**Biodiversity change (type and direction)**	**Mechanisms of biodiversity change**	**Infectious disease case studies**			
			Spillover layers affected	**Disease impacts**	**No. in Figure 1**	**References**
Agricultural expansion & intensification	Functional diversity (decreased)	Loss of large consumers increases rodent richness and abundance	Pathogen prevalence in wildlife host	Increased prevalence of Bartonella in rodents in Kenya	1	[33]
	Landscape diversity (decreased)	Resources become limited, pushing animals into human modified landscapes	Pathogen prevalence in wildlife host; human exposure to pathogen	Increased prevalence and spillover (zoonotic transmission) of *P. knowlesi* in Borneo	2	[63]
Urbanization	Ecosystem phenological diversity (decreased)	Resources become limited, pushing migrating animals to form resident populations in human modified landscapes	Pathogen prevalence and shedding in wildlife host; human exposure to pathogen	Increased prevalence, shedding, and spill of Hendra virus	7	[21]
Climate change	Functional diversity (increased)	Polar species replaced by migrating nonpolar species (via predation and resource competition)	Wildlife host density & distribution; pathogen survival & spread; human exposure to pathogen	Increased spillover risk of rabies in Alaska as a polar reservoir of rabies (Arctic fox) is being replaced by a more human-landscape adaptable reservoir species (red fox)	3	[120,125]
	Taxonomic and interaction diversity (increased)	Drought and reduction in water resources leads to increased density and diversity of hosts around shared water resources	Wildlife host density & distribution	Increased spillover risk of *E. coli* in Botswana	4	[130,131]
Invasive species	Taxonomic, functional, and interaction diversity (decreased)	Introduction of Burmese python reduces abundance of large- and medium-sized mammals	Human exposure to pathogen	Increased spillover risk of Everglade virus in Florida as mosquito disease vectors feed on rodent reservoirs more frequently	5	[136,137]

Wildlife trade	Taxonomic, genetic, functional, interaction, and landscape diversity (decreased)	Removal of wild, mostly large-bodied animals (via hunting, trapping, transfer, killing) or overfishing directly reduces abundance and diversity of terrestrial and marine wildlife species	Wildlife host susceptibility to infection; pathogen shedding in wildlife host; pathogen survival and spread; human exposure to pathogen	Increased spillover risk of Ebola in the Congo Basin as demand for wild meat from small-bodied mammals such as bats (Ebola reservoirs) increases (hunters and preparers of the bushmeat are exposed to bat bites, scratches, or blood)	6	[169,171,173,174]
Wildlife trade, Urbanization	Taxonomic and interaction diversity (increased)	Wildlife markets aggregate novel assemblages of hosts, increasing host richness that is unique to markets and the food supply chain	Wildlife host density & distribution, susceptibility to infection, and pathogen shedding	Increased wildlife susceptibility to infection, reservoir density, pathogen shedding and spread of SARS viruses	8	[162,166,167]

Table 2. Examples of ongoing biodiversity and sustainability initiatives that could potentially incorporate spillover prevention. Generality No. refers to the numbers (1–4) of the generalities described in section "Incorporating concepts of ecological diversity to mitigate spillover risk," which may be considered applicable for the biodiversity initiatives included in Table 2.

Initiative	Year founded	Description	Biodiversity goals	Potential health goals?	Potential extensions for preventing spillover	Generality No.	References
The Bonn Challenge	2011	Launched by the Government of Germany and IUCN to reduce deforestation and promote ecosystem restoration.	Obtain pledges for 150 million hectares of degraded and deforested landscapes globally on which to begin restoration by 2020 (which was successfully reached in 2017) and 350 million hectares by 2030.	Improve human health, wellbeing and livelihood by conserving and restoring degraded or deforested landscapes (no mention of infectious disease burden or spillover *per se*).	Landscape restoration of wildlife habitat, especially for large-bodied predators and consumers, could potentially help reduce spillover risk driven by increase in rodent abundance due to competitor and predator release related to agriculture and deforestation.	1–3	[175]
Convention on Biological Diversity (CBD)	1992	A list of goals (2020–2050) for sustainable nature-based solutions for improving planetary health and human wellbeing, set by the United Nations.	Address mitigation of biodiversity loss and anthropogenic disturbances.	Improve human health and well-being (no mention of infectious disease burden or spillover *per se*).	The CBD handbooks, including in 2020, do not mention actionable next steps for implementing nature-based solutions. How nature-based solutions may target spillover prevention merits further investigation.	1–3	[195,223]
Convention on International Trade in Endangered Species (CTES) of Wild Fauna and Flora	1973	A global agreement (182 countries) to regulate the international wildlife trade, and ban trade of endangered species.	Support surveillance efforts to track species under threat in the international wildlife trade, and control illegal wildlife trade activity.	Mission statement does not include the prevention of spillover (or improving human health or wellbeing).	CITES could adopt a pathogen screening regulation scheme to be implemented by all of its country members to prevent the global spread of emerging diseases, which may also hurt endangered wild populations.	2,4	[189,224]
Thirty-By-Thirty Resolution to Save Nature	2020	Part of a global effort, spearheaded by the Wyss Campaign for Nature, National Geographic Society, and over 100 organizations.	The Natural Resources Defense Council proposed a "commitment to protect nature and life on Earth" urging the US federal government to conserve at least 30% of	Mission statement does not recognize the additional human health benefits of reduced spillover risk via the proposed conservation efforts (e.g., conservation	Wildlife corridors would aid conservation of natural predators and large consumers, which could help reduce spillover risk of zoonotic disease where predators keep reservoir	1–3	[176,177,225,226]

			US lands and 30% of ocean regions by the year 2030.	of wildlife habitat and corridors for safe passage of wildlife between intact habitats).	populations in check (e.g., rodents) or where corridors help migrations of large herbivores (e.g., caribou) reducing brucellosis risk.		
Payments for Ecosystem Services (PES) Program in Costa Rica	1997	PES requires those who benefit from ecosystem services to compensate stewards of these services (e.g., landowners keeping forests intact should be compensated for the services their forests provide, such as carbon sequestration, clean air, and clean rivers).	Forest conservation and restoration aimed to improve biodiversity conservation and other recognized ecosystem services (e.g., watershed services, carbon sequestration, and landscape beauty).	PES programs do not explicitly include infectious disease or spillover prevention.	Spillover prevention could be embedded in existing efforts (or be introduced as its own ecosystem service). PES schemes that conserve contiguous and diverse forests could potentially benefit spillover prevention by reducing density of small-bodied mammal reservoir hosts, and intact forests serve as carbon sinks (thereby mitigating climate change effects on spillover).	1–3	[178,179]
Project Finance for Permanence (PFP)	2010	A model that includes restoring and conserving contiguous intact ecosystems. PFP programs, e.g., Amazon Region Protected Areas (ARPA), are funded by foundations, NGOs (e.g., WWF) and government agencies.	Aims to improve the abundance and management of intact ecosystems. ARPA intends to create, consolidate, and maintain a 60 million hectare network of protected areas in the Brazilian Amazon.	Although not a specific PFP objective, ARPA has likely reduced cases of malaria transmission in the Inner Amazon by slowing the rate of deforestation. This example highlights the potential joint benefits of the PFP model for conservation and public health.	Spillover prevention is not yet incorporated in PFP programs, although they could be extended to zoonotic spillover prevention via similar mechanisms to PES programs.	1–3	[182,183,227]

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