Impacts of anthropogenic change on biodiversity affect disease spillover risk

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Abstract

The integration of biodiversity conservation and public health has gained significant traction, leading to new efforts to identify win–win solutions for sustainable development and health. At the forefront of these efforts is pin-pointing ways that biodiversity conservation can reduce risk of zoonotic spillover, especially given the consequences of pandemics and epidemics 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. One limitation has been a narrow focus on the relationship between infectious disease and species richness only, thus missing other relevant dimensions of biodiversity. Here, we review the literature, considering a broad scope of biodiversity definitions, to identify cases where zoonotic pathogen spillover is mechanistically linked to changes in biodiversity. Extending biodiversity to include other dimensions of it, such as functional diversity, landscape diversity, spatiotemporal diversity, and interaction diversity, allows us to identify potential relationships between biodiversity change and zoonotic spillover. By reframing the discussion of biodiversity and disease using mechanistic evidence while encompassing multiple dimensions of biodiversity, we work toward general principles that can guide future research and more effectively integrate the related goals of biodiversity conservation and spillover prevention.

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 (e.g., the Bonn challenge) 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 (see [1]). However, given the incomplete understanding of the mechanisms linking biodiversity to infectious disease, a clear vision of efficacy and pathways for win–win solutions are 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.

To date, the discussion around biodiversity and disease has been boxed into 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[10-14], this debate has largely focused on correlations between host species richness and reservoir host pathogen prevalence. However, the results of this research show that effects vary in magnitude and direction, rendering this approach inactionable for public health interventions and context-dependent. Here, we focus less on the narrow question of species richness and more on 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 present a number of opportunities where ongoing conservation initiatives could consider these mechanisms further in order to reduce disease spillover risks (Table 1, Figure 1).

Although biodiversity is often equated with species richness, biodiversity encompasses all forms of variability among living organisms and the ecological complexes of which they are a part[15]. For example, biodiversity includes the functional diversity of a community, habitat diversity of an ecosystem, and many more interdependent characterizations[15] (Box 1). At the same time, zoonotic spillover encompasses multiple, interconnected processes in which pathogens circulating in one host population cause infections in another[16,17] (Figure 1). Zoonotic spillover is affected by many upstream ecological processes before a pathogen actually spills into a human host, including reservoir host density, distribution, susceptibility, and pathogen prevalence, infectiousness, survival, dissemination, and host-human contact. Once in the recipient (human) host, a series of biological and epidemiological factors determine if onward transmission is possible[16,17,18,19] (Figure 1). To harmonize spillover prevention and biodiversity conservation, we need a clear mechanistic understanding of how increases and decreases in multi-faceted aspects of biodiversity, from cascading effects at population level to communities and ecosystems, influence all components of the spillover process (Figure 1).

This review of the literature 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 then review ongoing sustainability initiatives that could incorporate spillover prevention, emphasizing how reframing the discussion about biodiversity and disease may facilitate win–win outcomes.

Anthropogenic disturbance, biodiversity change, and disease spillover

Agricultural expansion & intensification

As of 2019, agricultural expansion and intensification were the leading causes of biodiversity loss[15]. Agricultural development fragments and clears previously extensive ecosystems, creating edge habitats that increase human encroachment with wildlife[20], homogenizing landscapes to reduce availability of natural resources for wildlife, and releasing pesticides, fertilizers, and antimicrobial compounds into the environment. All of these factors contribute to population declines or even local extinctions of several species[21-23] and may influence the dynamics of infectious diseases with an important environmental component in their transmission cycle[24].

Clearing intact ecosystems for agriculture, development of plantations, and other land modifications (including urbanization), drive the loss of large- and medium-bodied animals (i.e., defaunation) while supporting the persistence or growth of populations of small-bodied animals[25-28]. Recent research has made it clear that loss of functional diversity due to non-random patterns of defaunation has significant effects on zoonotic spillover risk. Increase in disease risk spillover due to change in functional diversity of animal communities may occur either 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 here after.

Small-bodied mammals are common pathogen reservoirs, with the rodent and bat orders containing the highest number of known zoonotic hosts[29- 32]. 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[33,34]. These traits, namely diet and habitat generalism with fast-paced life history, high population density and promiscuity with human settlements, are positively correlated with zoonotic reservoir status[30,35,36]. On a global scale, the richness and abundance of zoonotic hosts (especially birds, bats, and rodents) positively correlates with degree of human land management[35,37]. Local studies in Kenya, Tanzania, and Madagascar found that this change in functional diversity 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[14,38 ,39].

Shifts in functional diversity of ecological communities may be driven also by the loss of interactions among large, medium, and small bodied animals. In savanna ecosystems in Central Kenya, extirpation of large herbivores 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[40,41]. Predators of reservoir hosts and vectors might also exert a crucial role in modulating the risk of disease spillover for humans[10]. 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[42]— these findings have been linked to construction of large dams and subsequent increases in schistosomiasis transmission throughout Africa[43]. 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[44]. Further, predator loss might 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 small-mammal predators that control the abundance of rodents competent hosts for Lyme disease[11].

In general, land conversion can homogenize habitats, alter species distributions[45-47] and change contact patterns between wildlife and humans. The resulting decrease in diversity and availability of productive and undisturbed habitat can shift the distribution of reservoir species to aggregate at high densities near humans, increasing interspecific contact rates and contacts between humans, previously unencountered mammals, and vectors, thereby increasing potential for transmission. For example, *Plasmodium knowlesi* malaria is expanding in Malaysia and across Southeast Asia, partially due to forest loss and agricultural land conversion[48- 53]. Loss of diverse and undisturbed habitat has driven the primary *P. knowlesi* reservoirs, 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[54,55,53]. 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[53]. High profile zoonotic pathogens, such as Ebola virus, similarly spillover in forest fragments[56,57], calling into question the effect of landscape configuration and diversity on zoonotic spillover risk.

Lastly, loss of diverse habitat and skew in functional diversity towards favoring reservoir hosts may concurrently 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[58,59]. This also occurs in aquacultural waters[60], wastewater from antibiotic-treated crops[61], and effluent from wastewater treatment plants (WWTP)[62]. 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[63-67]. Global rates of AMR are on the rise, driven by the misuse of antibiotics in clinical settings as well as the areas described above, with an estimated 700,000 deaths worldwide caused by AMR bacterial infections[68]. Our current understanding of the propensity for diverse wild animal species to harbor AMR bacteria is limited, in part due to little sampling efforts to-date[69]. However, initial research shows that animal populations highly exposed or adaptable to human modified habitats have higher prevalence of AMR bacteria than animals with little to no contact with humans[70], suggesting they may be more competent reservoir hosts of these potentially infectious agents. Smith et al. [70] found that 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 such, diverse habitats may reduce the likelihood of birds becoming inoculated with and transmitting AMR bacteria. Diverse habitats may jointly decrease AMR risk by protecting croplands from livestock wastewater runoff[71]. The effect of biodiversity change on

AMR spillover is severely understudied but, given the threat of AMR bacteria to global public health[72], warrants significant attention [69,70].

Climate change

Species may respond to climate change through plasticity[73], rapid adaptive evolution[74], and altitudinal and latitudinal range shifts to the edge of their geographic range[75-,77]. Alternatively, species may undergo global extinction or, more frequently, local population extinctions[78,79]. Together these responses can drive biodiversity change in complex, nonlinear, and interdependent ways. In the absence of emigration, species ranges may shrink, which has been observed primarily in polar and montane species (reviewed [80]), or species may face extirpation or extinction (e.g., [81, 82]). Furthermore, the velocity of rising temperatures differs among regions of the world, affecting species and populations differently[83]. 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[84,85]. Plastic, adaptive, and local declines or extirpation responses are currently well researched[86-,88], with the amphibian decline being perhaps the most emblematic case[89], but rarely in the context of pathogen spillover.

The abundance of specialist species, and thus functional diversity, may decline with range shifts, especially at high latitudes, although taxonomic diversity of some systems may increase with range shifts[90-92]. 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[35,36 ,93], 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[94].

The Alaskan Arctic is currently exhibiting climate-induced shifts in host species, namely 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[95]; 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[96]. 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[97-99]. 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[100]. Further, because the larger-bodied red fox displays more aggressive behavior than the Arctic fox[95], 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.

Comparable to effects of direct land-conversion (e.g., agricultural expansion), climate change may reduce habitat diversity and subsequently increase the likelihood of cross-species transmission through increased habitat overlap and taxonomic diversity in confined areas[101]. For instance, the melting of sea ice alters, disrupts, or even prevents migration patterns of animals such as wild caribou[102], 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[103]. In water-stressed parts of Africa, extreme droughts can similarly force many animals that previously had little to no contact with one another (such as humans, wildlife, and livestock) to congregate at common water sources[104,105]. When water sources are more abundant, wildlife occupy heterogeneous landscapes characterized by different types of surface water (e.g., rivers, seasonal pans, lakes)[106-109]. In drought conditions, animals are forced to use the same watering hole where increased traffic and fecal loads reduce water quality. In Chobe National Park, Botswana, these patterns and processes are associated with increased loads of *E. coli,* the leading cause of diarrheal outbreaks[105]. Following drought events, heavy seasonal rainfall and flooding events mobilize pathogen-containing feces, subsequently leading to human diarrheal outbreaks in neighboring communities[110].

Invasive species

Invasive species (i.e., organisms introduced outside their natural range negatively impact native biodiversity, ecosystem services, or human-wellbeing[111]) present a significant threat to ecosystems. 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[112]. 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[113,114]. 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*), potentially increasing the risk of virus exposure to humans[114].

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[115]; crayfish on schistosome intermediate hosts[116]). 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[117]. 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[29, 39, 118-120], sharing pathogens with native species[121-123] or providing resources for reservoirs and/or vectors[124,120]. In these cases, biodiversity conservation via invasive species control may simultaneously reduce zoonotic spillover risk (see [120]). The same processes that drive species introductions, including global trade and travel, may also drive disease emergence, suggesting that win–win solutions might be possible, though potentially technically and politically challenging[125].

Wildlife hunting, trade, and consumption

One in five vertebrate species are impacted by trade[126], with some wildlife facing population declines and/or species extinction due, mainly or in part, to the impacts of legal and illegal wildlife trade (e.g., tigers, rhinos, elephants, sharks, and pangolins)[127,128]. 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[129]. While it is still trumped by the $300 billion-dollar legal wildlife trade industry, the majority of legal wildlife trade (78%) is still made up of wild caught animals as opposed to those reared in captivity[130].

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 *Y. pestis*, monkeypox virus, coronaviruses, HIV, Marburg and Ebola viruses[127, 128, 130-133]. However, in order to stop or mitigate the spillover process, we need to have a better understanding of the mechanisms linking the wildlife trade to the steps leading to 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 (i.e., hosts in which a pathogen can rapidly replicate to high concentrations) and/or humans (see refs in following sentence). Trade may also impact the spillover process by promoting pathogen shedding from animals because of unsanitary conditions during, and stress from, transportation and market[134-141]. 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[142-144]. 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[143-145]. 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[140]. 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.

The wildlife trade for human consumption can take on various forms, which in turn can interact to amplify the effects of overharvesting of wild animals. For example, the wild meat trade in Ghana, which has driven population declines of certain mammalian species in the last few decades, correlates with local declines in fish supply, probably due to overfishing off the coast[146, 147]. 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 otherwise coming into contact with bodily fluids of animals serving as reservoirs for many pathogens. In the Congo basin and other regions of pathogen emergence, wild meat serves as a protein source primarily in poor households, making the banning of wild meat a controversial topic[148], 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 HIV, Ebola, Marburg, and monkeypox viruses[135, 149, 150]. Indeed, phylogenetic analyses of HIV suggest that approximately 10 spillover events occurred over the past century before HIV caused a pandemic[151]. In Cameroon, simian foamy viruses regularly spill over and infect wild meat hunters, but no human-to-human transmission has yet been established[131].

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[152, 153]. As a result, preliminary research suggests that overharvesting of wildlife may influence the types of wild animals hunters and consumers are contacting; however, mechanistic links between change in composition of wildlife markets and zoonotic disease risk have not yet been established.

Urbanization

With almost 70% of the world's population expected to live in urban areas by 2050[154], the transition from rural to urban land-use is a complex and dynamic process likely to power the greatest landscape transformations of the 21st century. Urban areas are characterized by high human density and an almost completely built environment.

Land conversion can reduce temporal diversity of food sources, 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[155]. 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[156,16, 157]. 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 (horses) and humans[158]. Reducing temporal diversity of resources or prohibiting access to high quality seasonal food sources may also promote spillover with respect to agricultural conversion. For example, 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[159-162].

Further, the rural to urban transition diversifies local economies from dependence on local agriculture to trade of goods, services, and ideas with more distant places[163]. 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[164]. Drastic reduction of non-human adapted animals in completely converted land (i.e., cities) may reduce the frequency of spillover of novel zoonotic pathogens[20]. 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[165]. Then, in the rare case where the biology of the pathogen allows frequent human-to-human transmission (e.g., high infectivity to humans, asymptomatic transmission, aerosol transmission[18]), the large and dense human population found in cities can facilitate rapid pathogen spread, resulting in the largest epidemics[20] or even pandemics. Spread of novel zoonotic pathogens may be mitigated by increased health and subsequent reduced susceptibility in planned urban areas (i.e., built from a blueprint, with the city's future in mind)[166]. However, the opposite may be true in unplanned urban areas (i.e., built ad-hoc, 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[167, 164].

Emerging generalities of the effects of anthropogenic disturbance on disease spillover through biodiversity change

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 a broader range of changes in biodiversity than just species richness and composition, we collect enough literature to propose four general concepts that are potentially operationalizable in ongoing and developing biodiversity initiatives. 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. 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 generalities may be more or less applicable for different ecosystems and disease threats.

(1) Loss of spatially and temporally diverse habitat alters the distributions of reservoirs leading to increased overlap more with other vertebrate hosts, vectors, and humans (see *Agricultural expansion & intensification, Climate change,* and *Urbanization* sections). This generality suggests an opportunity: preserving and restoring large, contiguous, and heterogeneous habitats could minimize encroachment of humans and wildlife in their respective habitats, thus decreasing intraspecific contact rates and ultimately transmission among reservoirs. 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[168]. Further, targeted habitat conservation and restoration could encourage previous migration patterns by re-creating or maintaining temporal diversity of high-quality food sources, such as nectar resources for bats[16, 120]. However, in some cases, resource provisioning—through invasive species, crops, and even waste disposal practices—may reduce migration even when phenologically diverse habitats are available[169, 170]. 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.

Overall, studying the mechanistic effect of spatiotemporal habitat 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.

(2) Loss of large consumers and predators (change in functional diversity) can result in increased abundance of animals with fast growth rates and relatively small ranges, such as rodent reservoirs and vectors (see *Agricultural expansion & intensification*). Thus, habitat conservation, preservation, and restoration could simultaneously reduce the density and improve the health of wildlife as well as supporting populations of large predators and herbivores[153, 171, 172]. 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. More research is needed to understand the impacts large herbivores and predators have on zoonotic disease regulation, especially within and around these ecotones. If more evidence supports a beneficial effect of conserving predators and large herbivores for reducing spillover risk, conservation of predators and large consumers may offer another promising win–win situation.

(3) 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. As described previously, these animals are more likely to be zoonotic reservoirs (see *Agricultural expansion & intensification, Climate change*). Change in functional diversity towards synanthropic species has been observed across taxonomic groups of vertebrates (e.g., rodents and birds: see *Agricultural expansion & intensification*; carnivores: see *Climate change*). Similar effects have been observed for disease vectors in which generalists thrive in urban areas and have high capacity to transmit pathogens to humans[43, 173, 174]. 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[120].

(4) 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 (see *Invasive species, Wildlife trade,* and *Urbanization*). Overall, regulations and initiatives that reduce diversity of novel interspecific interactions should be adjusted to incorporate spillover prevention.

Despite these generalities, cases of disease spillover driven by biodiversity change (in turn driven by anthropogenic disturbances) are highly context-dependent. Further, 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[175,176], leishmaniasis[177], and Chagas disease[178], 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[179-184]. Thus, win–win solutions for alleviating zoonotic disease burden and conserving biodiversity should be evaluated based on specific knowledge of the ecological and social system contexts[1].

Biodiversity and sustainability initiatives can combat disease spillover

Our synthesis provides new research directions and avenues for management at the intersection of biodiversity conservation and global health and begins to focus on a mechanistic understanding of the links between environmental change, biodiversity, and infectious disease spillover. Solutions grounded in ecological understanding may also require attention to the social context: promotion of long-term funding for community conservation and sustainable livelihoods programs; legislation from global to local entities for spillover prevention; and local awareness of, and investments in, monitoring the impacts of human activities on biodiversity and spillover in understudied systems. Certain international initiatives are already working towards sustainable solutions for promoting both public health (including preventing disease burden) and conservation, such as the UN Sustainable Development Goals[185], Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) Nature's Contributions to People[186], IUCN Global Standards for Nature-Based Solutions[187], Bridge Collaborative[188], Pan American and World Health Organizations (PAHO/WHO) Climate Change and Health[189], Global Health Security Agenda[190], and the collaboration among Food and Agriculture Organization (FAO), World Organisation for Animal Health (OIE), and WHO (FAO-OIE-WHO Collaboration)[191].

Here, we describe some ongoing biodiversity and sustainability initiatives that could incorporate spillover prevention (e.g., to avoid unintended harms from biodiversity conservation or to broaden the benefits of biodiversity conservation), emphasizing how reframing the discussion about biodiversity and disease to focus on ecological understanding of mechanisms creates opportunities for synergistic solutions. Though biodiversity may not causally affect spillover in all cases, sustainable development efforts can still jointly benefit conservation and human health[192], and at a minimum, avoid unintended harms.

The Bonn Challenge

The Bonn Challenge was launched by the Government of Germany and IUCN in 2011. Its goal was to 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[193]. This Challenge recognizes the benefits conserving and restoring degraded or deforested landscapes makes to human health, wellbeing, and livelihood. However, the Challenge does not address any potential effects of infectious disease burden or spillover directly. Where pledges lead to successful landscape-scale restoration of wildlife habitat, especially for large-bodied predators and consumers, the effort could potentially help reduce spillover risk driven by biodiversity change (e.g., increase in rodent abundance due to competitor and predator release) related to agriculture and deforestation (see *Agricultural expansion & intensification*).

Convention on Biological Diversity

The United Nations' Convention on Biological Diversity (CBD) proposes a list of goals between 2020 and 2050 for nature-based solutions (NbS) for benefitting planetary health and human health[194,195], defined as: "actions to protect, sustainably manage and restore natural or modified ecosystems that address societal challenges effectively and adaptively, simultaneously providing human well-being and biodiversity benefits." This clearly encompasses win–win solutions for human health and biodiversity conservation.

However, the CBD handbooks, including in 2020, do not mention actionable next steps for implementing such proposed interventions or even what they are[195]. Further, human health or well-being is not clearly defined, and there is no mention of infectious diseases. However, these goals do address mitigation of biodiversity loss and the anthropogenic pressures mentioned above. Thus, there should be potential for efforts led by CBD to also target spillover prevention, which merits further investigation.

Convention on International Trade in Endangered Species

In 1973, 21 countries signed a global agreement called the Convention on International Trade in Endangered Species (CITES) of Wild Fauna and Flora to regulate the international wildlife trade, and ban trade of endangered species. Today, the CITES agreement is being implemented by 182 countries and the European Union to regulate the trade of more than 35,000 species[196]. CITES supports surveillance efforts to track species under threat in the international wildlife trade, and works together with law enforcement from wildlife organizations, national parks, customs, and the police force to control illegal wildlife trade activity. However, the stated mission of CITES does not include the prevention of spillover. Only a few CITES country members use strict veterinary import border controls for animals. Further, there are no global regulations on pathogen screening related to the international wildlife trade. Conceivably, 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 (see *Wildlife hunting, trade, and consumption*), especially since emerging diseases may also hurt endangered wild populations[136]. Another possible synergistic effort that could prevent zoonotic spillover and preserve wildlife and biodiversity would be to reduce legal (and prevent illegal) commercial overfishing. CITES recognizes the necessity to control bycatch of threatened species, such as the critically endangered vaquita porpoise in Chinese and Mexican waters[196]. Fisheries collapse driven by overfishing has been associated with elevated bushmeat trade (see *Wildlife hunting, trade, and consumption*) in other parts of the world. Further investigations are warranted to unravel connections between various forms of wildlife exploitations and their downstream effects on spillover.

Thirty By Thirty Resolution to Save Nature

This initiative is part of a global campaign called the Campaign for Nature, spearheaded by the Wyss Campaign for Nature, National Geographic Society, and over 100 conservation organizations[197]. In 2020, the Natural Resources Defense Council (NRDC) proposed a 30x30 "commitment to protect nature and life on Earth" urging the US federal government to conserve at least 30% of US lands and at least 30% of ocean regions by the year 2030[198, 199]. Currently, the US protects only 12% of lands and 26% of its surrounding ocean areas[200]. The Biden administration announced its support for this goal in 2021[200]; however, the document written by the Agriculture, Commerce, and Interior Departments does not recognize the additional health benefits of reduced spillover risk via the proposed conservation efforts[201]. For example, the document proposes conservation of wildlife habitat and corridors for safe passage of wildlife between intact habitats. This would aid protection and maintenance of preserves and areas of intact habitat, as well as restoration and conservation of natural predators and large consumers. Conceivably, such biodiversity outcomes could help reduce spillover risk of zoonotic disease in the US where large-bodied mammals keep reservoir populations in check (e.g., rodents, see *Agricultural expansion & intensification*) or where corridors help migrations of large-bodied herbivores (e.g., caribou and brucellosis, see *Climate Change*).

Payments for Ecosystem Services Program in Costa Rica

The idea behind the Payments for Ecosystem Services Program (PES) effort is to let those who benefit from ecosystem services (e.g., biodiversity conservation, watershed services, carbon sequestration, and landscape beauty) compensate stewards of these services. For example, landowners keeping forests intact should be compensated for the services their forests provide to users downstream (e.g., carbon sequestration, clean air, clean rivers)[202]. PES schemes have been applied globally[203], with many successful programs implemented on the local, regional, and countrywide level in South America[203].

The government of Costa Rica was the first to implement a nation-wide PES program in 1997, which is funded through taxation (e.g., fossil fuel taxes), tariffs, and contracts with the industry (e.g., private hydro-electric producers), and loans from the World Bank and Global Environmental Facility Grant[204]. In addition to landowner compensation for their land's ecosystem services in Costa Rica, Indigenous territories were included as priority areas for conservation[205].

PES programs do not explicitly include spillover prevention. However, spillover prevention could be embedded in forest conservation and restoration aimed to improve biodiversity conservation and other recognized ecosystem services or be introduced as its own ecosystem service. PES schemes that conserve contiguous and diverse forests could potentially benefit spillover prevention in multiple ways. For example, density of small-bodied mammal reservoir hosts may decrease (see *Agricultural expansion & intensification*), and intact forests serve as carbon sinks thereby mitigating downstream effects of climate change (see *Climate change*). For programs centered around preserving and restoring forest, providing service suppliers with alternative income may further reduce contact with zoonotic disease reservoirs and vectors. However, service providers are not necessarily adequately compensated in Costa Rica[206], so schemes should be improved to offer improved, sustainable livelihoods. Conversely, PES schemes that promote sustainable forest management and agroforestry could theoretically increase spillover risk for some zoonotic diseases and should be planned with care. Increased disease risk may result from provisioning animals with high abundance and preferable resources, creating habitat for vectors, and from humans more frequently entering forested areas[207]. In these cases, zoonotic spillover may be better managed through other ecological interventions (e.g., barriers that limit human exposure to pathogens shed from reservoirs)[208] or vector management.

Project Finance for Permanence

Project Finance for Permanence (PFP) is another model that includes restoring and conserving contiguous intact ecosystems[209]. These projects are funded by a diverse set of donors, including local and global governments, private foundations, and private sector companies, and brokered and managed by NGOs (e.g., WWF) and government agencies. Examples of successful programs include the Amazon Region Protected Areas (ARPA), the Great Bear Rainforest Project, and Forever Costa Rica[210, 210]. Each project aims to improve the abundance and management of intact ecosystems, although at different capacities. The ARPA intends to create, consolidate, and maintain a 60 million hectare network of protected areas in the Brazilian Amazon (3x larger than all US National Parks combined). The Great Bear Rainforest Project supports 21 million acres (~8.5 million hectares) while promoting sustainable development among the area's First Nation People. The Forever Costa Rica Project has worked to maintain funding of and improve management of existing protected areas. Although not a specific program objective, ARPA has likely reduced cases of malaria transmission in the Inner Amazon by slowing the rate of deforestation[211]. 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.

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 to, or even thrive in, these new environments. Because these species tend to be better hosts for zoonotic pathogens, these landscape modifications increase 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.

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[212]. Another possibility could be lack of appreciation for the upstream mechanisms in the human-environmental system by which ecological changes can affect animal health and well-being which can, in turn, affect spillover. Wildlife hosts are not just containers and mixing vessels for zoonotic diseases; when exposed to stress from anthropogenic activities. 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[213, 214]. Thus, studies of biodiversity conservation and human health are needed to interrogate mechanisms by which environmental change (stressors) affecting wild animal health may lead to changes in the process of disease spillover to people and domestic animals. There is a need for spatially and temporally replicated field studies incorporating biodiversity change, pathogen dynamics, and wildlife host immunology[168, 214] in addition to human health outcomes.

Anthropogenic drivers of biodiversity change interact in complex ways, including synergies, direct and indirect effects and complex feedbacks. The combined impacts among many different anthropogenic disturbances may exacerbate the effects of biodiversity change on spillover risk. For example, defaunation is caused by many anthropogenic drivers (i.e., wildlife trade, climate change, agricultural intensification, and invasive species), which may additively, multiplicatively, or synergistically drive defaunation[26, 215], with downstream effects on ecosystem function and zoonotic spillover risk[216]. For instance, tropical land use change leading to deforestation and fragmentation negatively impacts the medium and large mammals of rainforests in Southeast Mexico, while promoting the proliferation of small mammals (rodents, many of them zoonotic reservoirs). Such fragmentation in turn facilitates additional hunting and poaching, which exacerbates defaunation and, in turn, increases exposure of humans to these disease hosts[216]. Very likely this synergy land use change-overexploitation will be further complicated by the changes in climate regime this topographically complex tropical area will experience. Moreover, feedback exists between spillover outcomes and anthropogenic activity, ultimately altering the outcomes for biodiversity conservation efforts. For example, spillback from humans to wildlife or other animals (reverse zoonosis (e.g.,[217])) or fear of secondary spillovers may alter disease dynamics and potentially suppress anthropogenic activities that drive biodiversity loss[211]. Thus, research involving the combined effects of multiple drivers of biodiversity change and its relationship with spillover is an agenda that warrants further efforts.

The world today 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, we urge biodiversity conservation efforts to also incorporate actions to prevent spillover into existing programs. The issue of 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 win–win interventions that prevent zoonotic spillover while protecting biodiversity.

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Tables, Boxes, and Figures

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 examples described by [218]:

- Genetic diversity: Aspects of genomic variability, including nucleotide, allelic, chromosomal, and genotypic.
- Taxonomic diversity: The number and relative abundance of taxa (e.g., species, genera, and onward). Disease-diversity relationships are typically described within the context of species richness.
- Phylogenetic diversity: Relationships among taxa based upon phylogenetic distance (i.e., amount of time the most recent common ancestor of both taxa.
- Spatial or temporal diversity: Rates of turnover of taxa through space and time.
- Interaction diversity: Characteristics of the network of linkages, such as abundance and variation in type and strength, defined by biotic interactions, including competition, facilitation, predation, and contact.
- Landscape diversity: Number, relative abundance, and distribution of different habitat types within a landscape (i.e., habitat 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.

Table 1. Case studies of mechanisms connecting anthropogenic disturbance with biodiversity change and its downstream effects on infectious diseases. 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	40
	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	53
Climate change	Spatiotemporal 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	95, 100
	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	105, 110
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	114
Wildlife trade	Taxonomic, phylogenetic, genetic, functional, spatiotemporal, 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	147, 149, 152, 153

Urbanization	Temporal diversity of habitats (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	16
Urbanization, Wildlife trade	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 (and human–human transmission)	Increased wildlife susceptibility to infection, reservoir density, pathogen shedding and spread of SARS viruses	8	140, 144, 145

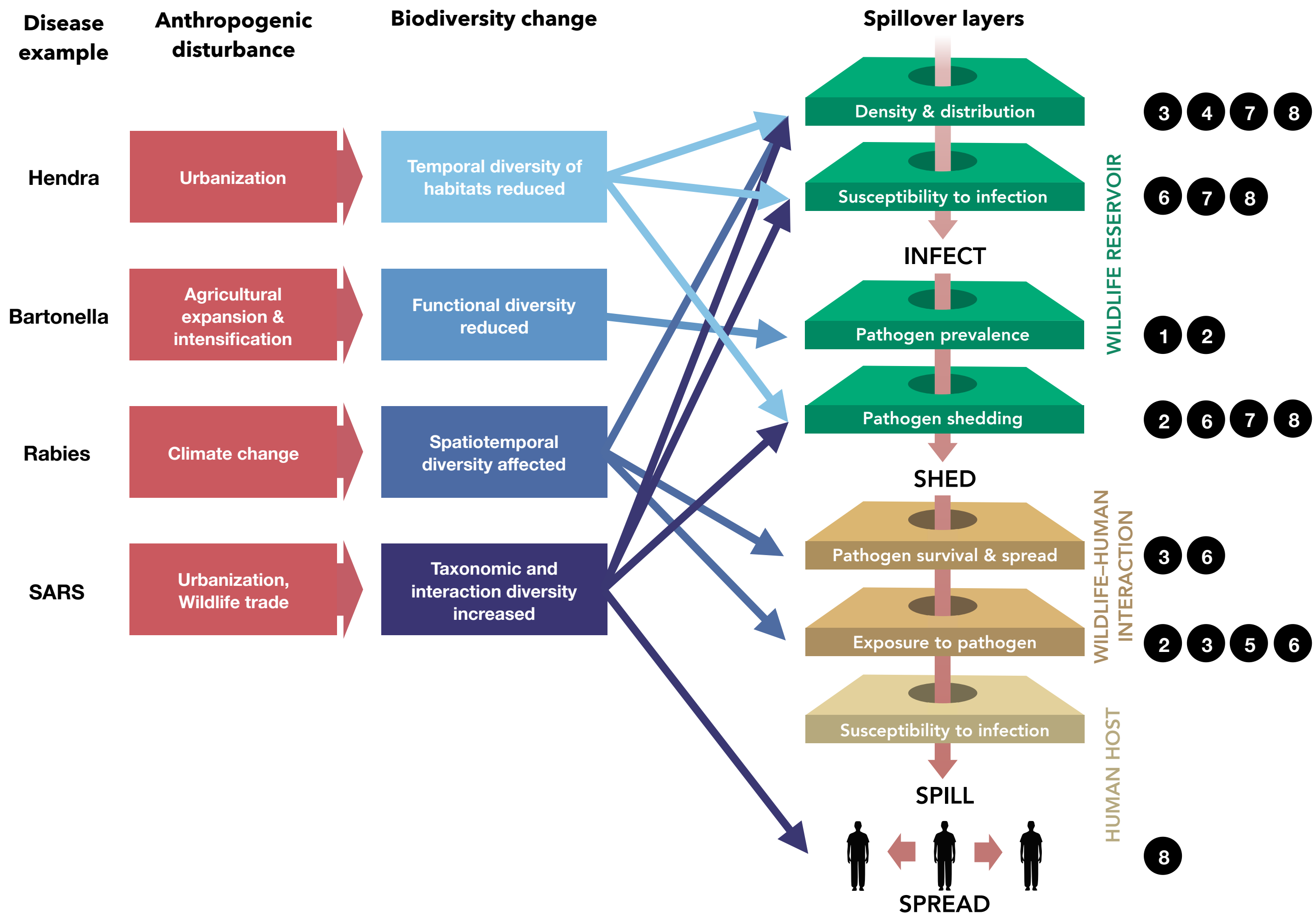

Figure 1. The anthropogenic disturbance, biodiversity change, and spillover cascade. To understand mechanisms connecting anthropogenic disturbance with spillover via biodiversity change, it is imperative to investigate how anthropogenic disturbance impacts biodiversity, and how those effects drive the 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.