

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

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22 **Abstract**

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

38 Introduction

39 The COVID-19 pandemic has brought the threat of zoonoses to the forefront, creating widespread
40 demand for managing ecological sources of disease spillover and emergence. Prior to this
41 pandemic, increasing recognition of the ties between healthy ecosystems and human health were
42 beginning to garner support of global conservation initiatives and spurred the United Nations'
43 (UN) adoption of sustainable development goals (the 2030 Agenda). Zoonotic spillover prevention
44 is a biosecurity imperative with a patent connection to the human–wildlife interface; thus, efforts
45 are underway to identify win–win solutions for biodiversity conservation and zoonotic disease
46 management¹. However, given the incomplete understanding of the mechanisms linking
47 biodiversity to infectious disease spillover, a clear vision of efficacy and pathways for win–win
48 solutions for health and the environment is needed. Increased attention to, and resources for,
49 zoonotic disease prevention make it an opportune time to study the mechanisms connecting
50 changes in biodiversity with zoonotic disease spillover, and to identify (potentially synergistic)
51 solutions for biodiversity conservation and global health.

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

65 Biodiversity encompasses all forms of variability among living organisms and the ecological
66 complexes of which they are a part; these different forms of variability have long been studied and
67 summarized into related but alternative definitions of biodiversity by other ecological fields¹⁷ (Box
68 1). Change in taxonomic diversity, including species richness, is often an observable outcome of
69 changes in other types of biodiversity that more explicitly guide conservation efforts such as the
70 loss of functional groups, changes in interaction networks, and heterogeneity in habitat
71 composition. Identifying how these underlying axes drive proximate changes in ecosystem
72 processes like disease transmission, is critical for responding to anthropogenic change^{10–16}.
73 Biodiversity can mechanistically affect spillover through several pathways as zoonotic spillover is
74 influenced by many ecological processes before a pathogen actually spills over into a human host,
75 including reservoir host density, distribution, susceptibility, and pathogen prevalence,
76 infectiousness, survival, dissemination, and host–human contact^{18,19} (Figure 1). Once in the
77 recipient (human) host, a series of biological and epidemiological factors determine whether
78 onward transmission is possible^{18–21} (Figure 1). To harmonize spillover prevention and
79 biodiversity conservation, a clear mechanistic understanding is needed of how increases and

80 decreases in multiple aspects of biodiversity, from individuals to populations to communities to
81 ecosystems, influence various spillover processes (Figure 1).

82 This review focuses on how infectious disease systems change with shifts in biodiversity,
83 highlighting case studies that suggest causal mechanisms (Table 1, Figure 1). We group case
84 studies based on the leading International Union for Conservation of Nature (IUCN)-classified
85 threats to biodiversity. While examples that mechanistically link environmental change to zoonotic
86 spillover via at least one metric of biodiversity change are scarce, our review identifies emerging
87 generalities across disease systems and anthropogenic disturbances. We find the best support for
88 an influence of functional, interaction, ecosystem phenological, and landscape diversity on
89 spillover risk but recognize that there are additional dimensions of biodiversity not explicitly
90 studied that are likely to influence spillover (e.g., genetic diversity²²). Within our description of
91 the generalities, we identify ongoing sustainability initiatives that could incorporate spillover
92 prevention, emphasizing how reframing the discussion about biodiversity and disease may
93 facilitate win–win outcomes for health and the environment.

94 **Anthropogenic disturbance, biodiversity change, and disease spillover**

95 *Land conversion, agricultural intensification, and urbanization*

96 As of 2019, agricultural expansion and intensification were the leading causes of biodiversity
97 loss¹⁷. Agricultural development fragments and clears previously intact ecosystems, creating edge
98 habitats that increase human encroachment on wildlife, homogenizing landscapes to reduce
99 availability of natural resources for wildlife, and releasing pesticides, fertilizers, and antimicrobial
100 compounds into the environment. Urbanization, characterized by built environments, similarly
101 clears intact ecosystems while increasing air, water, light, and land pollution²³. Moreover,
102 urbanization significantly increases human density: 70% of the world’s population are expected to
103 live in urban areas by 2050²⁴. All of these factors contribute to population declines or even local
104 extinctions of species^{25–27} and may influence the dynamics of infectious diseases with an important
105 environmental component in their transmission cycle²⁸.

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

115 Small-bodied mammals are common pathogen reservoirs, with the rodent and bat orders
116 containing the highest number of known zoonotic hosts^{40–43}. Certain taxa of small-bodied animals
117 are likely to predominate in human-modified landscapes due to traits that make them adaptable to
118 living in proximity to humans^{44,45}. These traits, including diet and habitat generalism with fast-
119 paced life history, high population density and proximity with human settlements, are positively

120 correlated with zoonotic reservoir status^{12,34,41}. On a global scale, the richness and abundance of
121 zoonotic hosts (especially birds, bats, and rodents) positively correlate with degree of human land
122 modification^{34,46}. Local studies in Kenya, Tanzania, and Madagascar found that this change in
123 functional diversity, so that communities are dominated by animals with traits conducive to
124 adaptation to human environments, increases zoonotic disease risk: rodent communities in
125 croplands had a higher proportion of competent zoonotic reservoir hosts and higher prevalence of
126 zoonotic pathogens than in unmanaged areas^{16,35,47}.

127 Loss of functional diversity of ecological communities may be driven also by the loss predators
128 and competitors that help regulate populations of reservoirs hosts and vectors. Land conversion
129 can drive the replacement of large herbivores with small herbivores, altering the overall effect of
130 herbivores on the plant community and ecosystem as a whole^{33,48}. In savanna ecosystems in
131 Central Kenya, exclusion of large herbivores through fencing, an experimental simulation of what
132 often occurs with agricultural intensification, resulted in changes in the plant community and
133 competitive release of small herbivores, leading to the increase in abundance of competent rodent
134 hosts (*Saccostomus mearnsi*) and prevalence of *Bartonella* and vectors^{33,49} (Table 1, Figure 1).
135 Predators of reservoir hosts and vectors might also exert a crucial role in modulating the risk of
136 disease spillover for humans^{10,11}. In Senegal, the construction of the Diama dam in 1986 to prevent
137 saltwater intrusion and support agriculture intensification blocked the migration of native predators
138 (the giant river prawn, *Macrobrachium vollehoveni*) that consume snail vectors and free-living
139 *Schistosoma* spp., resulting in increased transmission of vector-borne parasites to humans³⁶—
140 these findings have been linked to construction of large dams and subsequent increases in
141 schistosomiasis transmission throughout Africa³⁸. In terrestrial zoonotic disease systems, the
142 presence of leopards may decrease risk of rabies transmission to humans by preying on stray dogs
143 in Mumbai, India³⁷. Further, predator loss can trigger significantly more complex trophic cascades.
144 The loss of wolves in the Northeastern USA was followed up by an increase in coyotes, which in
145 turn led to a dramatic reduction of predators of small-mammals that control the abundance of
146 rodents competent hosts for Lyme disease¹¹. This release of competent rodent reservoir hosts from
147 predation has been linked to expansions in Lyme disease in the last two decades^{10,11}.

148 In general, land conversion for agriculture can affect landscape diversity (Box 1), thereby altering
149 species distributions and changing contact patterns between wildlife and humans^{50–52}. Landscape
150 diversity can be described as compositional diversity, including patch type diversity, and
151 configuration diversity, including number, size, and arrangement of patches. These aspects of
152 landscape diversity have nonlinear and complex responses to anthropogenic change⁵³. As many
153 existing biodiversity initiatives center around land conservation and restoration, including
154 landscape diversity in the biodiversity–disease discussion is crucial for identifying synergistic
155 solutions for biodiversity conservation and preventing zoonotic spillover. Within monocultures,
156 all metrics of landscape diversity are reduced. However, in relation to intact ecosystems moderate
157 agricultural conversion has various effects on patch type diversity, decreases patch size and thus
158 variation in patch size, and increases the distance among intact habitat patches^{54–56}. Fragmenting
159 of habitat into small patches can shift the distribution of reservoir species to aggregate at high
160 densities near humans, increasing contacts between humans, previously unencountered mammals,
161 and vectors, thereby increasing potential for transmission⁵⁷. For example, *Plasmodium knowlesi*
162 malaria is expanding in Malaysia and across Southeast Asia, partially due to forest loss and
163 agricultural land conversion^{58–63}, which drives the primary reservoir hosts, long-tailed macaques

164 (*Macaca fascicularis*) and pig-tailed macaques (*Macaca nemestrina*), to occupy small forest
165 fragments within or next to agricultural areas where they overlap with anthropophilic mosquito
166 vectors and people⁶³⁻⁶⁵. This shift in distribution not only increases the density of reservoirs,
167 potentially increasing transmission among reservoir hosts, but also increases potential for
168 macaque–vector–human transmission⁶³ (Table 1). High profile zoonotic pathogens, such as Ebola
169 virus, similarly spill over in forest fragments^{66,67}, highlighting the links between changes in
170 landscape configuration and diversity on zoonotic spillover risk.

171 Shifts in landscape diversity that skew functional diversity towards favoring reservoir hosts may
172 additionally increase the risk of antimicrobial resistant (AMR) zoonotic spillover. Runoff from
173 antibiotic-fed livestock forms wastewater lagoons where diverse bacteria mix and face strong
174 selective pressures to develop and share, via horizontal gene transfer (HGT), genes conferring
175 resistances to those antibiotics^{68,69}. This also occurs in aquacultural waters⁷⁰, wastewater from
176 antibiotic-treated crops⁷¹, and effluent from wastewater treatment plants⁷². Wildlife that contact
177 polluted waters or soils can pick up these AMR bacteria and transport them to both neighboring
178 and distant croplands or livestock operations where they can spill over to people⁷³⁻⁷⁷. Global rates
179 of AMR are on the rise, driven by the misuse of antibiotics in clinical settings as well as in
180 agriculture, with an estimated 700,000 deaths worldwide caused by AMR bacterial infections⁷⁸.
181 While research efforts on wild animal reservoirs of AMR bacteria are severely limited⁷⁹, initial
182 research shows that animal populations proximate or adaptable to human modified habitats have
183 higher prevalence of AMR bacteria than animals with little to no contact with humans⁸⁰, perhaps
184 due to higher host competency and/or exposure rates to these potentially infectious agents. Smith
185 et al.⁸⁰ found that the prevalence of AMR bacteria in agricultural areas decreased as the amount of
186 native habitat increased, possibly due to reducing contact rates of birds with livestock runoff. As
187 a result, landscape composition and configuration may reduce the likelihood of birds becoming
188 inoculated with and transmitting AMR bacteria. Landscape diversity may jointly decrease AMR
189 risk by protecting croplands from livestock wastewater runoff and by providing vegetation that
190 acts as natural ecosystem filters⁸¹. The effect of biodiversity change on AMR spillover is severely
191 understudied but, given the threat of AMR bacteria to global public health⁸², warrants significant
192 attention^{79,80}.

193 Further, land conversion can reduce the phenological diversity of natural ecosystems and food
194 sources (i.e., ecosystem phenological diversity, defined in Box 1), which can cause nomadic and
195 migrating species to forgo migration in favor of occupying the same habitat year-round. In some
196 cases, formation of resident populations may shift reservoir host dynamics to alter zoonotic
197 spillover risk, particularly when loss of seasonal, high-quality natural resources is paired with
198 provisioning of non-seasonal, subpar food⁸³. For example, loss of optimal winter resources, at
199 least in part due to habitat loss, drives reservoir hosts (*Pteropus* spp.) of Hendra virus from large
200 nomadic groups that track seasonally abundant nectar sources into small resident groups feeding
201 on permanent, suboptimal food within and around cities^{21,84,85}. Food stress may promote viral
202 shedding; simultaneously, the redistribution of reservoir hosts into smaller yet more abundant
203 colonies in human-dominated systems increases the likelihood of the virus spilling into
204 amplifying hosts (i.e., hosts in which a pathogen can rapidly replicate to high concentrations, for
205 example horses in this case) and humans⁸⁶. Similarly, agricultural conversion has limited the
206 availability of high-quality winter resources for elk. Large populations are now supported by
207 lower-quality supplemental feeding, which reduces migration and promotes high density

208 aggregations, thereby increasing the spread of *Brucella abortus* among reservoir hosts and
209 potentially spillover to livestock⁸⁷⁻⁹⁰. Climate change may further exacerbate loss of
210 phenological diversity and interrelated shifts in animal movement, however, this has not been
211 explicitly linked to zoonotic spillover⁹¹.

212 Finally, the rural to urban transition diversifies local economies from dependence on local
213 agriculture to trade of goods, services, and ideas with more distant places⁹². Through trade with
214 rural areas, urbanization interacts with other threats to biodiversity, such as introduction of
215 pathogens through the wildlife trade and introduction of invasive species, to drive changes in
216 zoonotic spillover⁹³. Drastic reduction of non-human adapted animals in completely converted
217 land (i.e., cities) may reduce the frequency of spillover of novel zoonotic pathogens⁹⁴. At the same
218 time, interactions between urbanization and other anthropogenic disturbances creates
219 circumstances for pathogen introduction, especially if pathogens can be sustained via human–
220 human transmission. For example, urban centers serve as hubs for long-distance shipping, with
221 urban wildlife markets often containing higher densities and diversity of wildlife. Thus, urban
222 wildlife markets create unique assemblages of species subsequently increasing the likelihood of
223 novel cross-species transmission⁹⁵. Then, in the rare case where the biology of the pathogen allows
224 frequent human–human transmission (e.g., high infectivity to humans, asymptomatic transmission,
225 aerosol transmission¹⁹), the large and dense human population found in cities can facilitate rapid
226 pathogen spread, resulting in the largest epidemics⁹⁴ or even pandemics. Spread of novel zoonotic
227 pathogens may be mitigated by increased health and subsequent reduced susceptibility in affluent
228 urban⁹⁶. However, the opposite may be true in unplanned urban areas or urban areas designed to
229 oppress groups of people (i.e., without centralized infrastructure and equitable distribution of
230 resources) where human health might be compromised by increased pollution, lack of affordable
231 healthcare, and limited access to healthy food and clean water^{93,97}.

232 *Climate change*

233 Species may respond to climate change through plasticity⁹⁸, rapid adaptive evolution⁹⁹, and
234 altitudinal and latitudinal range shifts to the edge of their geographic range¹⁰⁰⁻¹⁰². Alternatively,
235 species may undergo local population extinctions, range shifts, or even global extinction¹⁰³⁻¹⁰⁷.
236 Further, the velocity of rising temperatures differs among regions of the world, affecting species
237 and populations differently¹⁰⁸. Together these responses can drive biodiversity change in complex,
238 nonlinear, and interdependent ways. Here, we focus on case studies of range shifts in response to
239 rapid anthropogenic climate change, as it is the most immediately observable impact of climate
240 change on wildlife hosts harboring zoonotic pathogens^{109,110}. Plastic, adaptive, and local declines
241 or extirpation responses are currently well researched¹¹¹⁻¹¹³, with the amphibian decline being
242 perhaps the most emblematic case¹¹⁴, but they are rarely connected to pathogen spillover.

243 The abundance of different species with certain traits or ecosystem functions (e.g., diet, habitat,
244 activity patterns, etc.), and thus functional diversity, may decline with range shifts, especially at
245 high latitudes, although taxonomic diversity (Box 1) of some systems may increase with range
246 shifts¹¹⁵⁻¹¹⁷. This is largely attributed to generalists outnumbering specialists in systems impacted
247 by global change, as generalists are able to thrive in a variety of ecological conditions, including
248 human modified landscapes, while specialists need specific resources and/or habitats to survive.
249 At the same time, correlative analyses suggest that zoonotic reservoirs are more likely to be

250 generalist species^{34,39,118}, as they are more likely to live in closer proximity to people and contact
251 a wider range of other host species. Further, climate-induced forest habitat loss may lead to an
252 increase in abundance of extreme generalists with zoonotic reservoir potential, as in the case of
253 the highly adaptable deer mice harboring Sin Nombre virus¹¹⁹.

254 The Alaskan Arctic is currently exhibiting climate-induced shifts in host species, with an increase
255 in the abundance of zoonotic hosts more likely to contact humans. Before contemporary climate
256 change, the ranges of two carnivores and rabies reservoir hosts, red and Arctic foxes, were
257 separated¹²⁰; however, with climate change the home range of the generalist red fox has expanded
258 northward, encroaching on the territory of the comparatively habitat-specialist Arctic fox¹²¹. Arctic
259 fox numbers were already in decline due to other effects of climate change, such as the loss of sea
260 ice and tundra habitat as well as loss of lemming prey, but red foxes are expediting this decline
261 through intraguild predation and competition for resources^{122–124}. As Arctic fox populations are
262 replaced by red fox populations, the red fox will become the primary reservoir for rabies spillover.
263 This shift in the reservoir community will likely increase epizootic peaks of rabies as immigrant
264 red foxes interact more with resident Arctic foxes, increasing both the transmission rate and the
265 overall density of susceptible individuals¹²⁵. Further, because the larger-bodied red fox displays
266 more aggressive behavior than the Arctic fox¹²⁰, and because it is more amenable to adapt to
267 human-dominated landscapes, contact rates between wild rabies reservoirs and dogs or humans
268 might increase, thus increasing rabies spillover risk (Table 1, Figure 1).

269 Climate change may reduce other dimensions of biodiversity beyond functional diversity. For
270 instance, climate change may reduce landscape diversity by reducing patch diversity and
271 subsequently increase the likelihood of cross-species transmission through increased habitat
272 overlap and taxonomic diversity in confined areas¹²⁶. For instance, the melting of sea ice alters,
273 disrupts, or even prevents migration patterns of animals such as wild caribou¹²⁷, increasing the
274 chance of intermingling among caribou and other wild or domestic ungulates. Thus, people who
275 rely on caribou and/or other livestock might be at higher risk of brucellosis spillover under a
276 warming climate in temperate regions¹²⁸. Similarly, in water-stressed parts of Africa, extreme
277 droughts can force many animals that previously used different water bodies and had little to no
278 contact with one another (such as humans, wildlife, and livestock) to congregate at common water
279 sources^{129,130}, increasing traffic and reducing water quality due to elevated fecal loads. In Chobe
280 National Park, Botswana, these patterns and processes are associated with increased loads of *E.*
281 *coli*, the leading cause of diarrheal outbreaks¹³⁰. Following drought events in and around Chobe
282 National Park, heavy seasonal rainfall and flooding mobilize pathogen-containing feces,
283 subsequently leading to human diarrheal outbreaks in neighboring communities¹³¹ (Table 1).
284 Further, these water sources have potential to serve as melting pots of antimicrobial resistant
285 bacteria and sources of novel pathogen emergence¹³².

286 *Invasive species*

287 Invasive species (i.e., organisms that establish and spread outside their native range) negatively
288 impact native biodiversity, ecosystem services, or human wellbeing, presenting a significant threat
289 to ecosystems¹³³. Through processes such as predation, competition, or environmental
290 modification, invasive species can drastically decrease the biodiversity of an ecosystem; an
291 estimated thirty species of invasive predators alone are responsible for at least 58% of all bird,

292 mammal, and reptile extinctions globally¹³⁴. Invasive species can indirectly impact infectious
293 disease by altering the structure and composition of the native community in ways that either
294 increase or decrease pathogen transmission.

295 Altering a native community to increase zoonotic spillover risk has been empirically demonstrated
296 for the Everglade virus, a mosquito-borne zoonotic virus. The introduction of the Burmese python
297 (*Python bivittatus*) to the Florida Everglades has led to large-scale declines in functional and
298 taxonomic mammal diversity due to precipitous loss of large and small-bodied mammals^{135,136}.
299 With loss of mosquito food sources due to python predation on deer, racoons, and opossums,
300 mosquito vectors of Everglades virus fed dramatically more on the primary reservoir host of the
301 virus, the hispid cotton rat (*Sigmodon hispidus*), resulting in higher rates of Everglade virus
302 infection in mosquitoes, and potentially increasing the risk of virus exposure to humans^{136,137}. The
303 Burmese python–Everglade virus case study is a clear example of the dilution effect (i.e., higher
304 taxonomic diversity of hosts reduces disease risk and the loss of that diversity increases disease
305 spillover risk), which can readily occur for vector-borne, zoonotic pathogens for which the vector
306 can take “wasted bites” (from a pathogen transmission perspective) on non-competent hosts, as is
307 the case here⁹.

308 In contrast, introduction of invasive species can reduce transmission of infectious disease from
309 vectors to people through predation on various vector life stages (larvivorous fish on malaria
310 vectors¹³⁸; crayfish on schistosome intermediate hosts¹³⁹). However, despite crayfish lowering the
311 risk of schistosomiasis by voraciously consuming snail intermediate hosts and free-living
312 parasites, invasive crayfish compromised other dimensions of human health by consuming rice
313 and degrading canal banks with their burrows¹⁴⁰. Consequently, in scenarios where invasive
314 species reduce disease risk there can still be a tension between biodiversity impacts of invasive
315 species and their specific ecological roles in infectious disease dynamics.

316 Invasive species may affect infectious disease dynamics by acting as vectors or reservoir
317 hosts^{40,47,141–143}, sharing pathogens with native species^{144–146}, or providing resources for reservoirs
318 and/or vectors^{143,147}. In these cases, biodiversity conservation via invasive species control may
319 simultaneously reduce zoonotic spillover risk¹⁴³. The same processes that drive species
320 introductions, including global trade and travel, may also drive disease emergence, suggesting that
321 win–win solutions for protecting ecosystems from species invasion and humans from pathogen
322 spillover might be possible, though potentially technically and politically challenging¹⁴⁸.

323 *Wildlife hunting, trade, and consumption*

324 One in five vertebrate species is impacted by trade¹⁴⁹, with some wildlife facing population
325 declines and/or species extinction due, mainly or in part, to the impacts of legal and primarily
326 illegal wildlife trade (e.g., tigers, rhinoceroses, elephants, sharks, and pangolins)^{150,151}. The illegal
327 wildlife trade is estimated to be the world’s second largest underground businesses (hypothesized
328 to be a \$5–20 billion-dollar industry) after narcotics¹⁵². The legal wildlife trade, estimated to be an
329 even larger business (\$300 billion-dollar industry), also poses a threat to biodiversity as the
330 majority of legal wildlife trade (78%) is composed of wild caught animals, as opposed to those
331 reared in captivity¹⁵³. The local increase or decrease of biodiversity, as well as novel contacts

332 between species that do not co-occur in the wild, as different species are being translocated via
333 trade may drive spillover and disease emergence, as explained below.

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

340 The wildlife trade highlights how anthropogenic pressures can increase spillover risk via a direct
341 increase in both taxonomic diversity and the number of interactions across taxa (i.e., interaction
342 diversity, defined in Box 1) on very small spatial scales. Throughout the supply chain, the wildlife
343 trade brings together high densities of species that typically would not contact each other in natural
344 habitats. These unique assemblages and interactions can promote cross-species transmission,
345 increasing the likelihood that a pathogen may be transmitted to amplifying hosts and/or
346 humans^{154,157–163}. Trade may also impact the spillover process by promoting pathogen shedding
347 from animals because of unsanitary conditions during, and stress from, transportation and
348 market^{154,157–163}. For example, the ancestor to SARS-CoV-1 is suspected to have been transmitted
349 from horseshoe bats (most likely *Rhinolophus sinicus*) to palm civets, two species that do not
350 interact in wild settings. However, palm civets served as amplifying hosts or as intermediate hosts
351 within wildlife markets, bringing the virus in closer proximity to humans^{164–166}. Seroprevalence
352 and virological testing surveys of civets on farms *versus* those brought to markets in Guangdong,
353 China suggest that palm civets were exposed to the virus at the end of the supply chain^{165–167}. A
354 study performed in Vietnam showed that coronavirus detection in field rats caught or reared for
355 human consumption more than doubled when testing field rats sold in markets, and further
356 increased by 10-fold when testing field rats sold or served in restaurants, compared with rats in the
357 wild¹⁶². Thus, the wildlife trade creates opportunities for increased transmission among multiple
358 wild animal species and puts humans in closer proximity to stressed and infected wildlife, fueling
359 the potential for spillover of pathogens (Table 1, Figure 1).

360 The wildlife trade for human consumption can take on various forms, including commercial
361 harvesting of wild animals on land and at sea, which in turn can interact to amplify the effects of
362 overharvesting, leading to a decrease of many types of biodiversity, such as taxonomic, genetic,
363 functional, interaction, and landscape diversity (Box 1). For example, the wild meat trade in
364 Ghana, which has driven population declines of some mammalian species in the last few decades,
365 correlates with local declines in fish supply, probably due to commercial overfishing off the
366 coast^{168,169}. Conceivably, during periods when the demand for wild meat is high, hunters and
367 people involved with the butchering and preparation of the meat expose themselves to a higher
368 risk of disease spillover from bites, scratches, and other contacts with bodily fluids of animals
369 serving as reservoirs for many pathogens. In the Congo basin and other regions where pathogens
370 have recently emerged, wild meat serves as a protein source primarily in impoverished households,
371 making the banning of wild meat a controversial topic¹⁷⁰, though genetic and epidemiological
372 evidence suggests that it has contributed to the rise of emerging diseases and recent outbreaks via
373 spillover from wildlife to humans of pathogens like Ebola (Table 1), HIV, Marburg, and
374 monkeypox viruses^{154,171,172}. In Cameroon, simian foamy viruses regularly spill over and infect

375 wild meat hunters, but no human–human transmission has yet been established¹⁵⁴. Conversely,
376 HIV has adapted to undergo human–human transmission, but phylogenetic analyses suggest that
377 approximately 10 spillover events occurred over the past century before HIV caused a pandemic,
378 suggesting that frequent spillover during bushmeat hunting was critical for its emergence as a
379 pandemic¹⁵¹.

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

387 **Incorporating concepts of ecological diversity to mitigate spillover risk**

388 While mechanistic research linking changes in biodiversity to zoonotic spillover risk is limited due
389 to the expense and logistical challenges of elucidating these relationships, by considering more
390 mechanism-based changes in biodiversity than species richness and composition, we collect
391 enough empirical examples to propose four general concepts that have potential to inform
392 biodiversity conservation. These generalities may motivate further integration of biodiversity and
393 zoonotic pathogen spillover research, potentially opening more avenues of funding as well as
394 incorporation of multi-disciplinary methods for collecting and analyzing data. To illustrate this
395 application of our synthesis, we identify ongoing biodiversity and sustainability initiatives that
396 could use these generalities to incorporate spillover prevention (e.g., to avoid unintended harms
397 from biodiversity conservation or to broaden the benefits of biodiversity conservation). Echoing
398 Halsey⁸, we distinguish between *generality*, that which is mostly considered true, and *universality*,
399 that which is considered true in all possible contexts. These four generalities (described below)
400 may be more or less applicable for different ecosystems and disease threats.

401 First, loss of spatially and phenologically diverse habitat alters the spatio-temporal distributions of
402 reservoirs, leading to increased overlap with other vertebrate hosts, vectors, and humans. This
403 generality suggests an opportunity: preserving and restoring large, contiguous, and heterogeneous
404 habitats could minimize harmful contact between humans and wildlife and between host species
405 that do not commonly interact (e.g., a reservoir and an amplifying host) while additionally reducing
406 the density of reservoir hosts and subsequent intraspecific contact and transmission. The Bonn
407 Challenge¹⁷⁵, Thirty-by-Thirty Resolution to Save Nature^{176,177}, Payments for Ecosystem
408 Services^{178–180}, and Project Finance for Permanence projects^{181–183} all include conservation and/or
409 restoration of natural ecosystems but do not incorporate spillover prevention in project design and
410 implementation (Table 2). Intact and diverse contiguous landscapes may also promote landscape
411 immunity, defined as ecological conditions that maintain and strengthen the immune system of
412 wild animals to reduce pathogen susceptibility and shedding, particularly for potential reservoir
413 species including bats and rodents^{184,185}. Further, targeted habitat conservation and restoration
414 could encourage previous migration patterns by re-creating or maintaining phenological diversity
415 of high-quality food sources, such as nectar resources for bats^{21,143}. However, in some cases,
416 resource provisioning—through invasive species, crops, and even waste disposal practices—may

417 reduce migration even when endemic, phenologically diverse habitats are available^{186,187}. More
418 research differentiating the impact of habitat restoration *versus* limiting human provisions (e.g.,
419 through clearing of invasive plants or better waste disposal management) is needed. Importantly,
420 some biodiversity conservation initiatives such as Payment for Ecosystem services in Costa Rica¹⁷⁹
421 include agroforestry, which could hypothetically increase human exposure risk to zoonotic
422 disease¹⁸⁸. In these cases, the effect of landscape diversity and specific agroforestry practices on
423 spillover should be considered so as not to put biodiversity conservation and public health at odds.
424 Overall, studying the mechanistic effect of landscape diversity and ecosystem phenological
425 diversity on each spillover process (Figure 1) should lead to new insights that can guide evidence-
426 based policy for both conserving natural ecosystems and reducing spillover risk.

427 Second, loss of large consumers and predators (changes in functional diversity) can result in
428 increased abundance of animals with fast growth rates and relatively small ranges, such as rodent
429 reservoirs and arthropod vectors. Regulation of poaching (e.g., via the Convention on International
430 Trade in Endangered Species¹⁸⁹ initiative), and habitat conservation, preservation, and restoration
431 of contiguous, intact ecosystems could support populations of large predators and
432 herbivores^{174,190,191}. In turn, predators and large consumers may be important in ecotones between
433 intact and anthropogenic landscapes, where they can regulate populations of small-bodied
434 reservoirs that thrive in human modified areas. The initiatives aimed to restore and conserve habitat
435 in Table 2 could be adapted to support populations of wildlife that help regulate rodent populations.
436 For example, the Thirty-by-Thirty Resolution to Save Nature^{176,177} proposes conservation of
437 wildlife habitat and corridors for safe passage of wildlife between intact habitats—this plan could
438 be improved by configuring habitats and corridors to best support populations of keystone
439 predators and large consumers in areas of zoonotic disease risk. More research is needed to
440 understand the impacts large herbivores and predators have on zoonotic disease regulation,
441 especially within and around ecotones. If more evidence supports a beneficial effect of conserving
442 predators and large herbivores for reducing spillover risk without increasing human–wildlife
443 conflict, conservation of predators and large consumers may offer another promising win–win
444 situation for environmental and human health.

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

460 Fourth, commercial wildlife trade, introduction of invasive species, and transportation of livestock
461 and companion animals are activities that increase interaction diversity, introducing more
462 opportunities for cross-species transmission among different species and increasing the chance of
463 new pathogens emerging that may have zoonotic spillover potential. The Convention on
464 International Trade in Endangered Species¹⁸⁹ aims to control the illegal wildlife trade but does not
465 include objectives that prevent spillover: adopting global regulations on pathogen screening and
466 ethical and sanitary animal husbandry standards in the international wildlife trade could be a
467 natural next step in advancing management of zoonotic spillover. Overall, regulations and
468 initiatives that reduce diversity of novel interspecific interactions should be adjusted to incorporate
469 spillover prevention.

470 Other international initiatives are currently working towards sustainable solutions for promoting
471 both public health and conservation, such as the UN Sustainable Development Goals¹⁹⁶,
472 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)
473 Nature's Contributions to People¹⁹⁷, IUCN Global Standards for Nature-Based Solutions¹⁹⁸,
474 Bridge Collaborative¹⁹⁹, Pan American and World Health Organizations (PAHO/WHO) Climate
475 Change and Health²⁰⁰, Global Health Security Agenda²⁰¹, and the collaboration among Food and
476 Agriculture Organization (FAO), World Organisation for Animal Health (OIE), and WHO (FAO-
477 OIE-WHO Collaboration)²⁰². The initiatives included in Table 2 have not yet incorporated
478 spillover prevention.

479 We emphasize that the initiatives described here must only be implemented based upon local
480 context, centered around the needs, demands, and culture of the local people. A number of global
481 restoration and conservation efforts have been critiqued as colonialist and thus detrimental to
482 vulnerable and marginalized groups of people. For example, the Bonn Challenge has been
483 critiqued for foresting historically savannah ecosystems, thereby impacting ecosystem function
484 and rangeland livelihoods²⁰³. Further, the Payment for Ecosystem services in Costa Rica has
485 been rebuked as not adequately compensating people for the service they provide²⁰⁴ and Thirty
486 by Thirty has been challenged for disproportionately, negatively impacting Indigenous
487 communities while failing to account for their outsized, positive effect on biodiversity .
488 These initiatives may be improved by creating context-dependent management plans that are
489 designed around and implemented by local communities and Indigenous groups. One way to
490 achieve this is through conservation of land via Indigenous Protected Areas (IPAs); while
491 defined differently depending on the country, IPAs generally are large areas of intact ecosystems
492 managed or co-managed by Indigenous groups. More than 46% of national reserves within
493 Australia are IPAs²⁰⁶, and a small but increasing proportion of protected land in Canada are IPAs
494 (e.g., Thaidene Nënë Indigenous Protected Area, the homeland of the Łutsël K'é Dene First
495 Nation)²⁰⁷. The United States and countries with similar Thirty by Thirty goals should and could
496 create similar protected areas. Another successful model is Health in Harmony's programs in
497 Borneo, Madagascar, and Brazil, which start with "radical listening" within rainforest
498 communities to co-develop community-based conservation and health programs that reduce
499 deforestation and provide affordable healthcare access²⁰⁸.

500 We additionally emphasize that biodiversity conservation is not a panacea for zoonotic spillover
501 prevention, and many systems are too complex or understudied to prescribe clear links between
502 biodiversity change and spillover risk. For example, highly diverse multi-host, multi-vector
503 systems such as West Nile Virus (WNV), Ross River virus^{209,210}, leishmaniasis²¹¹, and Chagas
504 disease²¹², require more studies to document ecological drivers of reservoir and vector abundances
505 and capacities to transmit disease. Further, reservoir host species that contribute most to
506 transmission may be variable along geographic and land-use gradients^{213–218}. Even when
507 conservation-related levers for spillover prevention exist, their impacts should be compared to
508 those of other approaches (including economic and biomedical) and implemented from a
509 community-based, environmental justice perspective. Thus, sustainable solutions for alleviating
510 zoonotic disease burden while conserving biodiversity should be evaluated based on specific
511 knowledge of the socio-ecological context¹.

512 **Conclusions and future directions**

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

527 Certain disease systems are either understudied or too complex to elucidate the effects of
528 biodiversity change on spillover risk. In addition, some components of the spillover process
529 (Figure 1) are better studied than others in the context of the impacts of biodiversity change. Based
530 on our review, the effects of biodiversity change on wildlife host susceptibility, pathogen shedding,
531 and pathogen prevalence in the reservoir for example (three important steps of spillover) are
532 understudied compared to human pathogen exposure (Figure 1). This may arise because wildlife
533 host susceptibility, pathogen shedding and prevalence are difficult to observe²¹⁹. Another
534 possibility could be lack of appreciation for how wildlife health—not just presence or absence—
535 may affect zoonotic spillover risk. When exposed to stress from anthropogenic activities, wildlife
536 hosts may experience suppressed immune systems, rendering them more susceptible to
537 opportunistic infections, more pathogen shedding, and altered behavior that increases their
538 exposure to pathogens^{185,220}. Thus, increased pathogen surveillance and health assessment in
539 wildlife may interrogate mechanisms by which environmental stressors affecting wild animal
540 health may lead to changes in the process of disease spillover to people and domestic animals.
541 Finally, there is an urgent need for spatially and temporally replicated field studies incorporating

542 biodiversity change, pathogen dynamics, and wildlife host immunology^{184,185} in addition to human
543 health outcomes.

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

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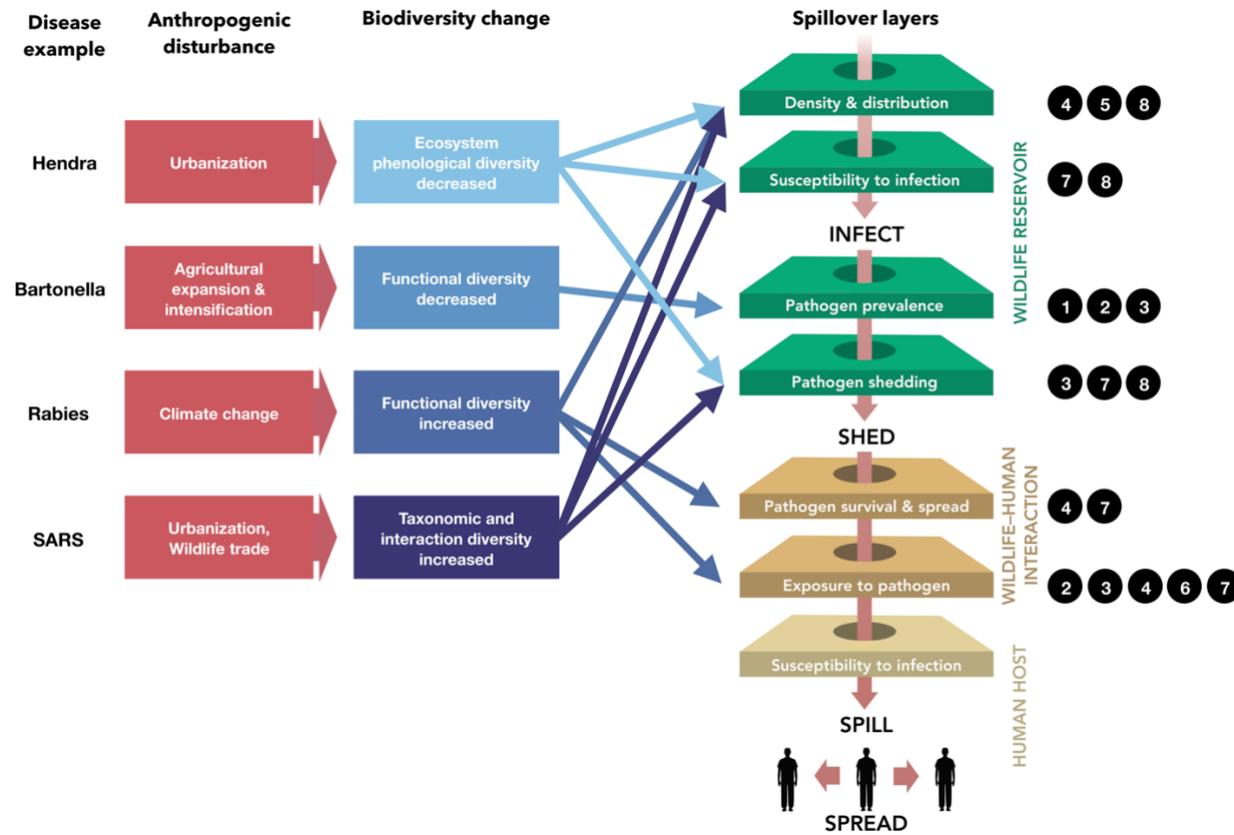
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Box 1. Examples of dimensions of biodiversity

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 by²², 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 community²²². 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



619

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

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 <i>P. knowlesi</i> 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	3	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)	4	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 <i>E. coli</i> in Botswana	5	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	6	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)	7	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 <i>per se</i>).	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 <i>per se</i>).	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 (CITES) 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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