LAND USE-INDUCED SPILLOVER: PRIORITY ACTIONS FOR PROTECTED AND CONSERVED AREA MANAGERS

Jamie K. Reaser[1,2,3*], Gary M. Tabor[1*], Daniel J. Becker[4], Philip Muruthi[5], Arne Witt[6], Stephen J. Woodley[7], Manuel Ruiz-Aravena[8], Jonathan A. Patz[9], Valerie Hickey[10], Peter J. Hudson[11], Harvey Locke[12], Raina K. Plowright[8]

[*]Joint first authors: jamiekreaser@gmail.com, gary@largelandscapes.org

[1]Center for Large Landscape Conservation, Bozeman, MT, USA
[2]Department of Environmental Science and Policy, George Mason University, Fairfax, VA, USA
[3]Department of Natural Resources, University of Rhode Island, Providence, RI, USA
[4]Department of Biology, University of Oklahoma, Norman, OK, USA
[5]African Wildlife Foundation, Nairobi, Kenya
[6]CABI, Nairobi, Kenya
[7]IUCN World Commission on Protected Areas, Canada
[8]Department of Microbiology and Immunology, Montana State University, Bozeman, MT, USA
[9]University of Wisconsin, Madison, USA
[10]Environment, Natural Resources and the Blue Economy Global Practice, World Bank, Washington, DC, USA
[11]Department of Biology, Pennsylvania State University, State College, PA, USA
[12]Beyond the Aichi Targets Task Force, IUCN World Commission on Protected Areas and Yellowstone to Yukon Conservation Initiative, Banff, Canada

ABSTRACT
Earth systems are under ever greater pressure from human population expansion and intensifying natural resource use. Consequently, micro-organisms that cause disease are emerging and the dynamics of pathogens in wildlife are altered by land use change, bringing wildlife and people in closer contact. We provide a brief overview of the processes governing 'land use-induced spillover', emphasising ecological conditions that foster 'landscape immunity' and reduce the likelihood of wildlife that host pathogens coming into contact with people. If ecosystems remain healthy, wildlife and people are more likely to remain healthy too. We recommend ten practices to reduce the risk of future pandemics through protected and conserved area management. Our proposals reinforce existing conservation strategies while elevating biodiversity conservation as a priority health measure. Pandemic prevention underscores the need to regard human health as an ecosystem service. We call on multi-lateral conservation frameworks to recognise that protected and conserved area managers are in the frontline of public health safety.

Key words: ecological countermeasures, ecological integrity, health, landscape immunity, land use-induced spillover, practices, protected and conserved areas, zoonotic disease

INTRODUCTION
Earth systems are under ever greater pressure from human population expansion and intensifying natural resource use. Human-induced impacts on the environment are now documented across nearly 75 per cent of the planet's land surface (Venter et al., 2016) and 66 percent of the marine realm (Diaz et al., 2019). Climate change and invasive alien species exacerbate these impacts. The consequences to human well-being of these human-driven challenges cannot be overstated; human health is inextricably linked to ecosystem health (Tabor, 2002; Patz et al., 2004; Evans et al., 2020).

This paper focuses on how land use change[1] drives the emergence and spread of micro-organisms (pathogens) that infect wildlife and humans with severe consequences for environmental, animal and human health. Pathogens that originate in vertebrate animals and cause disease in humans are known as zoonotic and these diseases are collectively referred to as zoonoses.

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When a pathogen crosses from one species to another (including to humans), the process is called spillover. When a pathogen spreads among humans, an outbreak is regarded as an epidemic (widespread in a particular population) or a pandemic (prevalent at epidemic levels across multiple countries with a global distribution). Spillback occurs when humans transmit pathogens back to domestic animals or wildlife.

The COVID-19 pandemic, caused by the SARS-CoV-2 virus, demonstrates society's inability to respond in a timely and effective manner to novel pathogens. The result is mass human suffering and mortality, bringing substantial moral, ethical and economic dilemmas. The most effective, cost-efficient and humane way forward is to keep wildlife healthy by keeping landscapes healthy (Andrade et al., 2020; Dobson et al., 2020; Lovejoy, 2020). As protected and conserved areas are the most widely used approaches to securing species, habitat and ecological integrity, they have a critical role to play in safeguarding public health. Hockings et al. (2020) call upon countries and sectors to work together to ensure that protected and conserved areas facilitate planetary recovery from COVID-19, while simultaneously advancing human and economic health and well-being.

We provide a brief overview of the processes governing land use-induced spillover, placing emphasis on ecological conditions that foster landscape immunity and reduce the likelihood of infected animals coming into contact with susceptible people. From our perspective, a 'healthy' ecosystem is one in which wildlife–pathogen interactions are in balance and wildlife are not overly stressed or concentrated together by land use-induced changes (Patz et al., 2004). If ecosystems remain healthy, wildlife and people remain healthy. We recommend practices for reducing the risk of future pandemics through protected and conserved area management. Our proposals reinforce existing One Health principles (Gibbs, 2014) and conservation strategies while elevating biodiversity conservation as a public health service. We call on multi-lateral conservation frameworks to recognise that protected and conserved area managers are in the frontline of public health safety (Stolton & Dudley 2010).

Agriculture is one of the most significant drivers of deforestation globally © Shutterstock

DEFINING LAND USE-INDUCED SPILLOVER AND OTHER KEY PROCESSES

Although pathogens (including bacteria, viruses and protozoan parasites) are a normal occurrence in biological systems and have important, perhaps undervalued, ecological functions where they have co-evolved with their wildlife hosts (Hudson et al., 2006; Gómez & Nicholas, 2013), environmental destruction and degradation can alter these established relationships. Land use change involving human-induced ecosystem change in any kind of habitat is a major driver of the transmission of pathogens from wildlife to humans (Brearley et al., 2013; Plowright et al., 2021). All species have a range of chemical, physical and biological conditions – environmental conditions – in which they thrive (or perish if conditions are insufficient or too extreme). When environmental conditions are no longer ideal, the relationship between micro-organisms and their hosts can change, sometimes leading to higher levels of infections.

Wildlife stressed by the environmental conditions associated with land use change can lose immunity and become more susceptible to zoonotic pathogen infection (Sapolsky, 2010; Becker et al., 2020; Nelson et al., 2020; Seiler et al., 2020). Stress can increase the likelihood that wildlife will release (shed) pathogens that lead to the infection of other animals of the same or different species, including humans (spillover). When land use change increases interaction between infected animals and people, it is more likely that zoonotic pathogens will cross over into human populations. The rate and scale of pathogen spread in human populations is largely driven by human social behaviour (the greater the contact rates among humans, the higher the likelihood of pathogen transmission) and pathogen biology (e.g., ability to transmit before symptoms are evident). Urbanisation and other land use changes increase human population density, thus increasing the risk of infection. Today, advances in human transport technologies and globalised consumer patterns spread

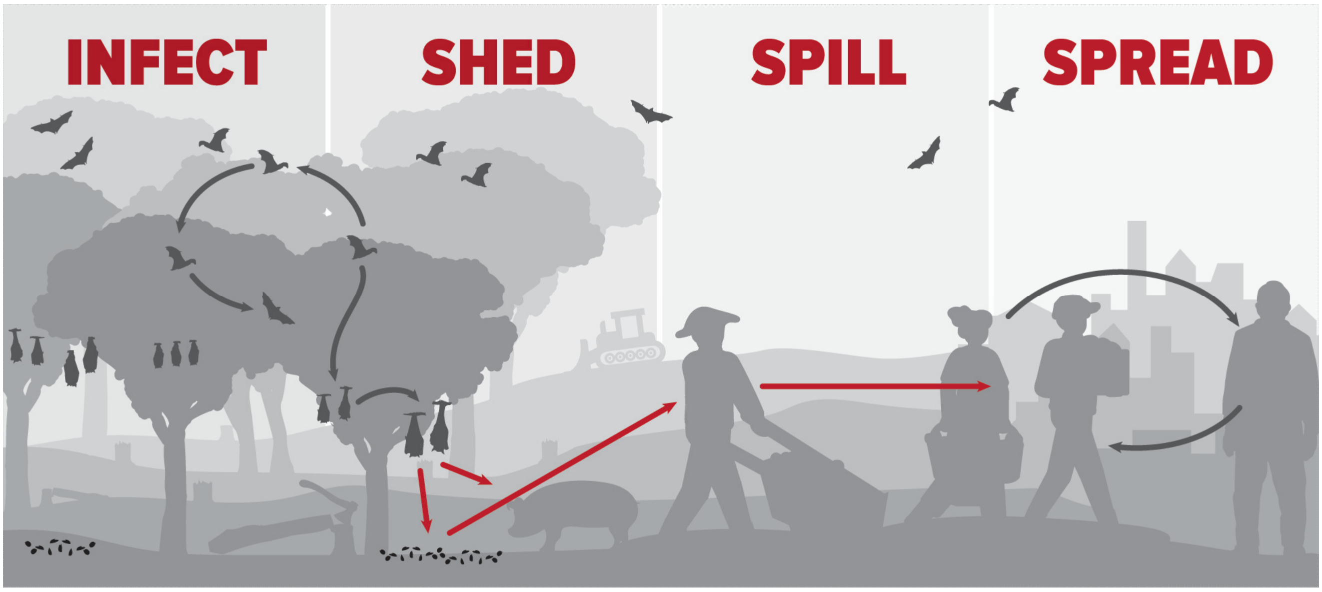


Figure 1. Land Use-Induced Spillover

Human activities that destroy and degrade ecological systems can trigger land use-induced spillover, the infect–shed–spill–spread cascade. Wildlife stressed by the environmental conditions associated with land use change can decline in immune function, thus becoming more susceptible to zoonotic pathogen infection. Stress can also increase the likelihood that wildlife will release (shed) pathogens in ways and locations that lead to the infection of other animals of the same or different species, including humans (spillover). When land use change increases interaction between infected animals and people, it is more likely that zoonotic pathogens will be transmitted into human populations. The rate and scale of pathogen spread in human populations is largely driven by patterns of human contact (social behaviour) and pathogen biology.

zoonotic pathogens faster and more extensively than before – making it possible for local land use events to have global-scale implications. Plowright et al. (2021) summarise this as the infect–shed–spill–spread cascade, and refer to it as land use-induced spillover. We provide a simple model of these pathogen dynamics in Figure 1. More elaborate models can be found in Plowright et al. (2021).

An animal or a person infected with a pathogen is referred to as a host. Pathogens shed by the host may spread to other hosts by one of three pathways (Plowright et al., 2017): 1) animal excreta (e.g., directly through saliva from a bite from an infected animal, such as in rabies, or indirectly through urine or faeces contaminating food, e.g., Nipah virus was spread by consuming date palm sap or Giardia from drinking contaminated water); 2) slaughter or butchering (e.g., Ebola virus was transmitted through preparation of bushmeat); or 3) a vector, usually an arthropod, such as a mosquito or tick, that bites an infected animal and then bites another animal (examples are dengue virus, Lyme disease and trypanosomiasis). A reservoir host is a wild animal that maintains the pathogen within its populations and serves as a source of infection, in some cases without making the animal sick (Viana et al., 2014). A recipient host receives the infection from another host. For zoonotic pathogens, recipient hosts are ultimately humans, but the infection can be transmitted via an intermediate or bridging host that has contact with the reservoir host and humans. Other species of wildlife or domestic animals, particularly livestock, can be intermediate hosts (Plowright et al., 2017).

Despite the severity of the implications for human health and well-being, land use-induced spillover is not a well-studied phenomenon across ecological systems (Reaser et al., 2020a; in press). However, research findings reveal that the relationships between land use change and wildlife disease are not easily generalised; different scenarios arise depending on the geographic location, ecosystem type, current and historical land uses, species of pathogens and animal hosts involved, the way the pathogens are transmitted, and animal–human dynamics of proximity (Brearley et al., 2013; Plowright et al., 2021). Land use-induced spillover is evidently a complex process in which land use change can affect many parts of the infect–shed–spill–spread cascade simultaneously. For example, forest fragmentation may drive changes in the relationship among species (trophic structure), increasing the abundance of reservoir hosts or vectors, and increased prevalence of infection. At the same time, people and wildlife are brought into closer proximity (Faust et al., 2017, 2018). To better inform land use management, Plowright et al. (2021) call for scientists across disciplines to collaborate in studying the mechanisms driving land use-induced spillover.

Reaser et al. (2020a) define landscape immunity as the ecological conditions that, in combination, maintain and strengthen the immune function of wildlife within an ecosystem. Messing et al. (2018) and Becker et al. (2020) propose that a high degree of landscape immunity should limit pathogen prevalence (e.g., via the dilution effect; Faust et al., 2017), enable wildlife to resist pathogen infection and minimise shedding. This will reduce pathogen exposure and spread among wildlife, and between wildlife, domestic animals and humans. Landscape immunity will prevent the infect–shed–spill–spread cascade, protecting animal and human health (see Figure 1 in Reaser et al., 2020a).

An ecosystem with high landscape immunity can be regarded as a 'healthy landscape' because it is intact enough that: a) pathogen populations are kept in check by sufficient numbers of predators and competitors; and b) wildlife can access the resources they need to remain healthy enough to resist or reduce pathogen infection (Patz et al., 2004). Although land use change is often thought of as large-scale ecological destruction, the more subtle invasion of non-native plants can also reduce animal fitness (Vilà et al., 2011). Figure 1 in Plowright et al. (2021) presents these highly complex dynamics in a relatively simple model of land use-induced spillover.

Contact patterns – the dynamics of proximity – between animals and people are also influenced by land use change. They affect the extent to which infected animals will expose other animals and people to shed pathogens. Understanding the dynamics of proximity among wildlife, domestic animals and human populations in various contexts poses a major challenge, but is critical to understanding the dynamics of emerging infectious diseases (Hassel et al., 2017). Muehlenbein (2016) reviews the spillover risk factors that result from human interactions with livestock, companion animals, animal exhibits and wildlife through both nature-based tourism and consumption. Primate–human contact is particularly problematic because primates host several pathogens deadly to humans and some human-originating pathogens can decimate wild primate populations via spillback.

TAKING STRATEGIC ACTION TO PREVENT LAND USE-INDUCED SPILLOVER

The following ten practices are intended to enable countries and sectors to work together to ensure that protected and conserved area management limits the risk of future pandemics, thereby protecting human health and economic well-being, including local livelihoods. The specific roles and responsibilities for implementation of these recommendations will vary across protected and conserved areas. We, therefore, refer to 'protected and conserved area managers' in general terms, recognising that the specific activities may need to be taken up by national and local governing bodies, donor agencies, natural resource specialists, biological and social scientists, veterinarians, educators, tourism operators, food vendors, waste managers, residents, visitors and neighbouring communities, among others.

Effective responses to land use-induced spillover may require: 1) changes in human distribution and behaviour; 2) shifts in land management principles, strategies, technologies, ethics and laws; and 3) a substantial, long-term investment in protected and conserved area restoration, expansion and connectivity. Effectiveness also depends on the willingness and ability to implement the practices below. This requires an understanding of: local socio-economic and cultural conditions; geographic and ecological factors; the epidemiology of pathogens, hosts and vectors; and the capacity of education, community-based cooperation, policy and law.

In response to COVID-19, Hockings et al. (2020) establish three principles and three phases of action on which to base management decisions for protected and conservation areas. We complement their framework with additional actions that place protected and conserved area managers at the forefront in preventing land use-induced spillover. We take a landscape-scale approach to zoonotic disease prevention through protected and conserved area management, but our recommendations are consistent with the full suite of nature-based solutions to COVID-19 advocated by leading conservation organisations (Global Goal for Nature Group, 2020). We provide additional research and management guidance addressing land use induced -spillover, based on Plowright et al. (2021), Reaser et al. (2020a) and Locke et al. (2019). Landscape management approaches to spillover risk reduction are part of a wider strategy for preventing the emergence of disease, which also includes ecological, veterinary and medical interventions (e.g., Sokolow et al., 2019), and policy initiatives, notably in controlling the wildlife trade (Reaser et al., 2020a).

Practice 1: Assess risk

Protected and conserved area managers have a public responsibility to understand and manage zoonotic spillover risks to the extent feasible. In some parts of the world, these risks may be substantial, while in other regions they are negligible (Jones et al., 2008). Zoonotic disease risk exists across terrestrial, freshwater and marine ecosystems, but varies as a function of the local ecology and patterns of human behaviour. Although knowledge of the distribution of zoonotic pathogens, disease emergence and spillover is in its infancy, increased investments in pathogen surveillance and related studies are elucidating patterns and trends that improve risk assessment capacity. Taxonomically, we know that rodents, bats and primates tend to act as zoonotic pathogen hosts, and that mosquitoes, ticks and some other arthropod groups commonly vector zoonotic pathogens (Luis et al., 2013; Olival et al., 2017). Areas rich in a diversity and abundance of these taxa warrant spillover risk analysis – particularly when the wildlife is stressed by land use change, there are large populations of species that can host zoonotic pathogens, and there is substantial risk of human exposure to these pathogens.

Studies of zoonotic pathogen prevalence in wild mammals have revealed that the risk varies geographically and with degrees of disturbance. Han et al. (2016) report fewer mammalian zoonotic diseases in very high latitudes. Allen et al. (2017) found that the risk of emerging zoonotic diseases is greatest in forested tropical regions experiencing land use changes and where mammal species richness is high. They present a global hotspot map of emerging zoonotic disease spatial variation. Johnson et al. (2020) found that the number of zoonotic viruses detected in mammalian species correlated with global species abundance, suggesting that virus transmission risk is higher from mammal species that have increased abundance and/or range because of changes in human-dominated landscapes. They found that domesticated mammal species, primates and bats carried the greatest risk of zoonotic virus infection. Populations of threatened wild mammal species that were reduced in number from habitat loss and exploitation carried a high diversity of zoonotic pathogens. More detailed studies of animal behaviour and biology are needed to understand the spillover mechanisms associated with these broad-scale geographical associations.

Human exposure and susceptibility to wildlife pathogens are the basis of zoonotic spillover risk. The likelihood of spillover at a particular location is thus a function of the probability that people will have direct contact with infected wildlife, indirect contact through wildlife body-fluids (e.g., excrement, saliva) or are bitten by a pathogen vector. Most often, the patterns of wildlife–human encounter at a particular protected or conserved area will vary over space and time, particularly in light of land use changes. Likewise, human susceptibility is spatio-temporally variable, and may also be influenced by socio-economic factors, for example people living in impoverished conditions may have health problems that make them particularly susceptible to pathogen infection (Muehlenbein, 2016). Estrada-Peña et al. (2014) reviewed how environmental conditions affect the distribution of zoonotic pathogens and their transmission to humans; they found that environmental change can modify the behaviour and relative importance of different pathogen host species, in turn affecting contact rates with humans. The risk of zoonotic spillover in protected and conserved areas may be affected by changes in environmental conditions at local (e.g., ecological succession or biological invasion influencing microclimate) or regional scales (e.g., climate change impacts on extreme weather events).

Human-association with domestic animals that host zoonotic pathogens, particularly certain mammal and bird species within and bordering protected and conserved areas, can greatly affect the risk of exposure to zoonotic pathogens. The presence of domestic animals that serve as intermediate hosts for zoonotic pathogens generally increases the risk of land use-induced spillover, especially if they are used for human consumption or where direct contact is routine (e.g., tuberculosis in cattle, Shury, 2015). The way domestic animals are managed can also increase host and vector populations. For example, rodents are frequently able to share animal feed, water and shelter (Stenseth et al., 2003). Standing water provided for domestic animals, or that forms in the hoof ruts or wallows created by domestic animals, can support mosquito larvae (Imbahale et al., 2011). Ways of using domestic animals to reduce zoonotic spillover risk are addressed under Practice 5.

Where agriculture is practised within and at the margins of protected and conserved areas, crop raiding by wildlife that host zoonoses can expose humans to zoonotic pathogens. Some primates are notorious crop raiders. Siljander et al. (2020) found that most farms in southeast Kenya experienced primate crop raids on a weekly basis. The primate species, crop type and distance from the forest to the nearest farm determined raiding patterns. In Uganda, crop raiding by primates was associated with transmission of gastrointestinal pathogens (*Escherichia coli*) to humans and livestock (Goldberg et al., 2008). In Australia, Flying Foxes (*Pteropus* bats) that have lost their winter nectar resources due to deforestation have begun feeding on fruit and other food in agro-urban landscapes, increasing the risk of Hendra virus spillover (Plowright et al., 2015). Land transformation that leads to grasses can increase the number of rodents and raise the risk of zoonotic diseases such as tularemia, hantavirus pulmonary syndrome and Lassa fever (Young et al., 2017). Where human food supplies are limited, people may hunt wildlife for supplemental protein thus becoming exposed to pathogens during butchering and consumption. In some cases, food scarcity drives people to consume diseased poultry and livestock, leading to outbreaks of disease caused by pathogens such as *Bacillus anthracis* (Katani et al., 2019).

The Food and Agriculture Organization of the United Nations (FAO), the World Organisation for Animal Health (OIE) and the World Health Organization (WHO) share responsibility to minimise the human health, animal welfare and socio-economic impacts associated with zoonotic disease. One of their goals is to mitigate potential health threats at the human–animal–ecosystem interface through early warning and robust risk assessments, provided through the Global Early Warning System for Major Animal Diseases Including Zoonosis (GLEWS).[2] Protected and conserved area managers can benefit from the early warning risk assessment guidance, tools and notifications made available nationally through GLEWS and the three administrating organisations. For example, the OIE has published guidelines for assessing the risk that non-native animals (including potential zoonotic hosts) may become invasive.[3]

Practice 2: Conduct surveillance

Surveillance involves the systematic collection, analysis, interpretation and dissemination of information about the occurrence of pathogens, or their clinical diseases, in animal or human populations. Effective surveillance is crucial for early detection and rapid response to emerging diseases, but is inadequate globally. For example, surveillance for zoonotic disease has focused on livestock or humans, rather than wildlife populations (Grogan et al., 2014), so knowledge of intervention opportunities is biased towards the 'downstream' elements of the infect–shed–spill–spread cascade.

The COVID-19 pandemic demonstrates the need for governments, donors and research institutions to overcome the social, technical and financial barriers to surveillance of wildlife species that serve, or may serve, as zoonotic pathogen hosts. The U.S. Agency for International Development's Emerging Pandemic Threats PREDICT program[4], which ran from 2009 to 2019, aimed to identify and map wildlife pathogens with zoonotic potential (Carlson, 2020). Protected and conserved area managers will be hampered in their ability to make risk-informed decisions unless priority is given to surveillance programmes, especially those that address the ecological dynamics of pathogens (Plowright et al., 2019) and the mechanisms driving land use-induced spillover.[5]

Zoonoses risk management strategies for primates living in proximity of human populations are vital. Long-tailed Macaque, Kuala Lumpur, Malaysia © Jamie Reaser

Protected and conserved area managers have vital roles to play in disease surveillance. Their intimate knowledge of the landscapes and species they manage can improve sampling rigour and help collaborating scientists to tease apart the complex ecological and social factors that influence pathogen distributions and biology (see Practice 10). It is thus vital that they are actively encouraged to report disease outbreaks to the appropriate veterinary and medical authorities as a standard task. Humans are put at risk if the fear of losing tourist income discourages such reporting and agencies need policies to stop this happening.

Practice 3: Protect protected and conserved areas

For reasons explained above, the highest levels of landscape immunity are likely to be associated with the least-disturbed landscapes (Reaser et al., 2020a). Fostering landscape immunity in protected and conserved areas should focus on ensuring a wide range of ecological structures and functions. This includes retaining a full complement of native species and their inter-relationships. For example, Terraube (2019) recommends the use of protected and conserved areas to

mitigate Lyme disease risk by encouraging a diverse array of tick predators (discussed further below).
Protected and conserved areas thus need to be protected in practice, not just in concept. Due to the increasing pressures on natural resources and limited budgets for protected and conserved area management, this may be difficult (Joppa et al., 2008), but it remains a necessary goal from environmental, animal and human health perspectives. Landscape-level conservation in which wildlife roams freely across protected and conserved areas helps gain natural space, maintain ecological connectivity, build ecological resilience and improve livelihoods of local communities. The most extensive assessments of the opportunities and challenges for landscape-scale conservation planning, with its implications for zoonotic pathogen spillover, may be those undertaken in Africa (e.g., Didier et al., 2011; Henson et al., 2009; Muruthi, 2004). However, a region-by-region assessment is warranted to synthesise findings and identify information gaps.

Effective site protection may require bold conservation targets and the prohibition of some land use activities within protected and conserved areas, especially logging and mining: such large-scale extractive resource uses require substantial infrastructure and often have long-term disturbance implications (Maron et al., 2018). Smaller scale activities – from tourism to wildlife poaching – may also need to be controlled within and around protected and conserved areas (discussed further below).

Protected areas and conserved areas are nested in a wider landscape and thus subject to ecological pressures that transcend their boundaries (reviewed in Hansen & DeFries, 2007). Invasive alien species can act as ecological stressors by adversely impacting the resources needed by native species of wildlife, for example, by outcompeting them for food, and making them more susceptible to pathogen infection and shedding. Invasive alien species (e.g., non-native rodents) can also become hosts of zoonotic pathogens or vectors (e.g., for non-native mosquitoes). Protected and conserved areas should therefore take preventative measures against the introduction and spread of invasive alien species, especially where there is substantial human presence (Dayer et al., 2020; Liu et al., 2020). Tu (2009) provides guidance for assessing and managing invasive alien species within protected and conserved areas.

Climate change is another stressor that transcends protected and conserved area boundaries. Elsen et al. (2020) point out that, at least in the terrestrial context, these static boundaries may actually undermine the potential to protect species under climate change scenarios. Protected and conserved area managers therefore need to develop adaptive management strategies to address the shifting capacity of their areas to maintain biodiversity, whilst taking into consideration that zoonotic pathogen, host and vector dynamics are expected to change within and around protected and conserved areas. Research thus far indicates that climate change is expanding the range of many zoonotic pathogens, particularly those vectored by mosquitoes (Manore et al., 2020).

Practice 4: Restore ecosystem health

Many protected and conserved areas are susceptible to anthropogenic pressures, mainly due to insufficient financial resources, lack of management capacity and poor governance (see review in Geldmann et al., 2019). Protected and conserved areas that have a history of land use disturbance and/or have suffered invasive alien species impacts may require strategic restoration interventions to secure biodiversity and human health. Restoration planning should include ecological and human health goals, with an emphasis on restoring landscape immunity. Aronson et al. (2016) review the needs and opportunities for restoration ecology to serve public health needs, emphasising the importance of the medical, veterinary and environmental sectors collaborating in this work. Plowright et al. (2021) also call for interdisciplinary collaboration to arrest land use-induced spillover by fostering greater landscape immunity. Social scientists should be included in such efforts so that the human dimensions of protected and conserved area management are properly addressed. For example, through cost-benefit analysis, Morlando et al. (2011) demonstrated that habitat restoration can pay for itself via the reduction of tick-borne disease. Similar analyses conducted in other zoonotic systems are needed to promote the value of protected and conserved area restoration to policy makers and donor agencies.

Keenleyside et al. (2012) provide extensive guidance for ecological restoration within protected and conserved areas. Here we emphasise two points that are likely to have substantial implications for landscape immunity, but are not typically addressed in protected and conserved area restoration strategies from the zoonotic disease perspective:

A. The size of the protected and conserved area at functional ecological scales is important in establishing landscape immunity and delivering ecosystem services, including the protection of human health. Ideally, protected and conserved area conservation should be integrated with the management of surrounding landscapes and with land use strategies, and supported by local communities (Lopoukhine et al., 2012). Over time, land use and climate change will require larger areas to be managed for ecological viability (Hanson & DeFries, 2007). Protected and conserved areas may need to be expanded to maintain landscape immunity within their borders.

In the context of zoonotic spillover, there are, however, at least two important caveats. First, the larger the landscape to be protected, the greater the likelihood that local human populations will need to be an integral part of the protected and conserved area management. Land use zonation can help address these issues. Further discussion is provided under Practices 6 and 7. Second, the expansion of protected and conserved areas may benefit some zoonotic pathogen host and/or vector populations by providing them with ideal habitat. For example, disease vectors like Tsetse Flies (*Glossina morsitans morsitans*) thrive in intact landscapes rather than landscapes which have been cleared of vegetation (Ducheyne et al., 2009).

B. Protected and conserved areas need to be managed to reduce the edge effects that occur at the boundary of two or more habitats. Edge effects are influenced by the geographic layout of protected and conserved areas and the land uses occurring at their margins. Increased edge effect (from a patchwork of varied land uses) can promote interaction among pathogens, vectors and hosts (Patz et al., 2004; Faust et al., 2018). In Uganda, the reduction of core areas and increased density of edges of forest patches were correlated with increased contact between humans and non-human primates in the communities around Kibale National Park (Bloomfield et al., 2020). Glass et al. (1995) have shown that edge effects can increase the prevalence of Lyme disease. Despommier et al. (2006) reviewed the role of ecological system boundaries (ecotones) on emerging infectious diseases, including zoonoses, and concluded that the human-created or modified ecotones may increase disease risks.

Practice 5: Maintain and restore connectivity

Many zoonotic pathogen hosts are highly adapted to human modified landscapes and may thrive in disturbed areas (Ostfeld & LoGiudice, 2003). For example, Langlois et al. (2001) found that infection by Sin Nombre virus (Hantavirus) in Deer Mice (*Peromyscus maniculatus*) was higher in fragmented habitats at more than 100 sites across Canada. In addition, Deer Mice moved faster across the landscape where there are patches of low-quality habitat, so increasing virus transmission. In Panama, Gottdenker et al. (2011) found that forest remnants within highly disturbed areas of the landscape may be sources for *Rhodnius pallescens*, a vector of Chagas disease. A similar pattern exists in India where Kysanur forest disease is associated with fragmentation that drives increased contact with ticks and greater incidence of disease (Purse et al., 2020).[6]

Since protected and conserved areas often provide species with resources that exceed what is available in the bordering landscape, wildlife diversity, abundance and density may be unnaturally high in isolated reserves, particularly if these areas are fenced. Where this happens, intra- and inter-species competition and crowding may increase the risk of zoonotic pathogens emerging and transmitting (Lebarbenchon et al., 2006). However, restoring ecological connectivity would allow organisms to meet their resource needs, with more space to move in response to the weather – and indeed the changing climate. This will avoid many of the issues associated with small populations, such as low genetic diversity. Hilty et al. (2020) provide guidance for conserving connectivity through ecological networks and corridors. On behalf of the Convention on Biological Diversity, Ervin et al. (2010) established guidance for integrating protected and conserved areas into wider landscapes and seascapes, as well as sectoral plans and strategies. Examples of how this has been actualised within protected and conserved area networks are available in Worboys et al. (2010) and Fitzsimons et al. (2013), for example.

However, there is also a risk that increased connectivity may facilitate pathogen spread through the increased mobility of their hosts and vectors (Hess, 1996). The effect of connectivity on pathogen spread depends on many factors, such as host movement rates in relation to pathogen infectious periods (Cross et al., 2005). High connectivity has facilitated the spread of wildlife diseases (e.g., pneumonia in Bighorn Sheep (*Ovis canadensis*); Cassirer et al., 2013), whereas low connectivity has been proposed as a driver of high Hendra virus prevalence in Pteropodid bats (Plowright et al., 2011). Fergusan and Hanks (2012) note that the use of park and veterinary fences to reduce zoonotic disease risk by separating wildlife, people and livestock is fragmenting African rangelands. However, when fences are removed, more widely roaming wildlife can spread zoonoses that cause hardship to rural communities and harm national livestock exports.

In South Africa, where genetic diversity has decreased in species of conservation concern due to population isolation, animals are sometimes translocated between protected and conserved areas. While this is intended to benefit the species, it may place the animals at increased risk of contracting zoonotic disease through interaction with wildlife at other localities. And unless they are shown to be disease-free before translocation – which can be difficult and expensive to do – there is a risk that the translocated species may transmit pathogens to wildlife in the destinations they are sent to (Cassirer et al., 2018).

Practice 6: Manage human activity in wildlife habitat

Recent research indicates that human activity in protected and conserved areas can have a greater impact on ecological integrity, and thus landscape immunity, than previously supposed. For example, Betts et al. (2017) found that the first acts of deforestation in tropical ecosystems can push a diversity of species closer to extinction due to loss of habitat and the land use activities that deforestation facilitates (e.g., hunting, farming, mining). These issues are largely addressed in the previous 'Practices'.

Since protected and conserved areas often support a higher diversity and abundance of wildlife than human-dominated landscapes, human activity within these areas may increase people's exposure to wildlife pathogens, as well as potentially transmitting human pathogens to wildlife (spillback), as in the case of gorillas infected by tourists or neighbouring communities (Dunay et al., 2018), and the possibility that humans may transmit SARS-CoV-2 to local bat communities (Olival et al., 2020). Other risks may also be associated with direct human–animal contact (e.g., rabies) or pathogen transmission via vector bites. In Colombia, increased human activity in forest habitats appears to be a major risk factor for leishmaniasis infection, which is spread via Sand Flies (*Phlebotomus perniciosus*; Weigle et al., 1993). In the northeastern United States, Lyme disease (*Borrelia burgdorferi*), transmitted by Blacklegged (Deer) Ticks (*Ixodes scapularis*), presents a risk to those who work and recreate outdoors (Mead et al., 2018). A university collaboration in the eastern United States[7] is underway to evaluate if tick bite frequency increases as people spend more time outdoors trying to avoid COVID-19 infection.

Domestic animal management is also an important part of mitigating the risk of human exposure to zoonotic pathogens. In the highest exposure risk situations, prohibitions on the possession of certain types of domestic animals may be warranted (e.g., non-human primates as pets or for tourist exhibition). Tethering ('leash') and containment (e.g., fencing, coops/sheds) may be sufficient for managing dogs, cats, livestock and poultry. When rodents are attracted to the food and structures associated with human activity, people may be exposed to zoonotic pathogens. Controls are needed on the feed and grain provided to domestic animals, and rodent trapping and euthanasia programmes may be necessary. In Ecuador's Galapagos Islands, Island Conservation and partners have worked with Floreana Island residents to control non-native rodent and cat populations that posed zoonotic disease risks, including toxoplasmosis, leptospirosis, cat scratch disease, cutaneous larva migrans, lymphocytic choriomeningitis, plague, hantavirus and salmonellosis (Hanson & Campbell, 2013).

There may also be opportunities to use domestic animals to reduce the risk of human exposure to zoonotic pathogens, a practice known as zooprophylaxis (Dobson et al., 2006). For example, Keesing et al. (2018) found that integrating livestock and wildlife in African savannahs can reduce tick abundance, thus protecting pastoralists and tourists from tick-borne diseases. Duffey et al. (1992) found that Helmeted Guinea-fowl (*Numida meleagris*) significantly reduced populations of Blacklegged Ticks in suburban lawns in New York State (USA): maintaining this species as domestic fowl may provide a relatively low-cost way to reduce Lyme disease risks. Landowners at the margins of Shenandoah National Park in central Virginia (USA) are increasingly interested in using Guinea-fowl to control tick populations on their properties (Reaser, pers. obs.). Care must be taken, however, that the domestic animals employed to reduce the risk of one disease do not amplify another by serving as hosts or becoming invasive, so driving environmental change and associated stress.

Often, education and social marketing are sufficient to help humans protect themselves from direct contact with wildlife or their bodily fluids (see Practice 9). However, protected and conserved area planning and policy also plays an important role. Protected and conserved area zoning can be used to define geographic areas for specific purposes, such as species conservation or recreation (Rotich, 2012). Zonation can be used to reduce zoonotic disease risk by reducing the likelihood of contact between animal hosts (wild and domestic) and people. For example, if human facilities associated with the protected and conserved area are concentrated near the reserve boundaries, this can help prevent human access and associated disturbance (wildlife stress) in core areas. It could also assist in limiting and concentrating trail and road infrastructure to protected and conserved area margins, thereby discouraging illegal entry for hunting (e.g., bushmeat; van Velden et al., 2020) or other purposes, and minimising the spread of invasive alien species.

Practice 7: Prevent wildlife from being drawn towards people

In order to reduce the risk of wildlife transmitting zoonotic pathogens to park managers, tourists and people living within and at the margins of protected and conserved areas, measures should be taken to prevent wildlife from being drawn to human activity, especially localities providing food and water for people. Although bites, crop raiding and the occupation of human dwellings by zoonotic pathogen hosts present obvious spillover risks, numerous more subtle but equally health-threatening issues arise from indirect contact with the saliva and excrement of wildlife. For example, on the Caribbean Island of Saint Kitts, Gallagher et al. (2019) found that invasive African Green Monkeys (*Chlorocebus aethiops sabaeus*) carried faeces containing zoonotic parasitic organisms on their hands and/or feet. Trichuris spp. eggs, Hookworm larvae and eggs, and Pinworm eggs were recovered from picnic tables frequented by tourists. A similar situation has arisen with free-ranging Baboons (*Papio cynocephalus* and *P. anubis*) in Kenya (Hahn et al., 2003).

Common measures taken within protected and conserved areas include: prohibiting visitors from feeding wildlife, requiring visitors to remain in vehicles, making sure that human food waste and excrement is not accessible to wildlife, and fencing wildlife out of agricultural, business and dwelling areas. In the case of Great Ape tourism, minimum viewing distances and requirements to wear N95 masks are employed (MacFie & Williamson, 2010). At Boabeng-Fiema Monkey Sanctuary in Ghana, Agyei et al. (2019) found that compensation from sanctuary proceeds, education and arresting poachers was an effective way of mitigating human–monkey conflict for all but the poorest communities. Hockings and Humle (2009) provide guidance for reducing conflict and disease between humans and Great Apes.

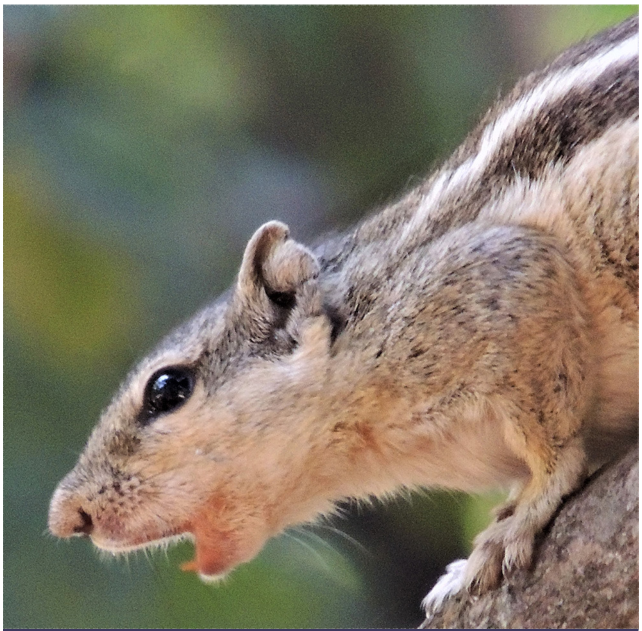
Establishment and fencing of protected areas to isolate biodiversity from human activities is one of the most popular methods for achieving this protection. Although fencing protected and conserved areas to isolate wildlife from human activity is widely used to reduce human–wildlife conflict (Massey et al., 2014), fencing poses pros and cons for zoonotic disease management. Some fences function as environmental stressors, facilitating land use-induced spillover (see Practice 4). In other situations, they may be an effective approach to mitigating zoonotic exposure risk from large mammals, but other approaches (e.g., chemical and biological control) will be needed to prevent vector bites. Protected and conserved areas could employ ecological fencing analogues using native vegetation. Jakes et al. (2018) review fencing as an animal management tool globally: they argue that managers need to understand the implications of 'fence ecology'.

It is also possible to use buffer zones to minimise human–wildlife interactions. Creative buffer zone designs can support protected and conserved area disease risk minimisation goals. Land management zoning regulations can limit human activities within and at the margins of protected and conserved areas (Schonewald-Cox & Bayless, 1986; Dudley, 2008).

Practice 8: Employ ecological countermeasures

There are a growing number of ecological management interventions that can prevent or reduce zoonotic disease outbreaks (Sokolow et al., 2019). Reaser et al. (in press) regard ecological countermeasures as highly-targeted, landscape-based interventions to arrest one or more of the elements of the land use-induced spillover infect–shed–spill–spread cascade. They believe that ecological countermeasures should complement reactive public health responses to disease emergence, such as quarantine and vaccines.

Plowright et al. (2021) propose strategic tree planting as an ecological countermeasure to prevent Hendra virus spillover in Australian agricultural landscapes. This project is made feasible because the Hendra virus system has been studied for decades and the process of pathogen transmission among primary hosts (fruit bats; *Pteropus* spp.), intermediate hosts (horses) and humans has been identified. The bats experience winter nutrition stress due to the loss of winter-flowering *Eucalyptus* trees and move into human-dominated landscapes to feed. Horses, the intermediate host of Hendra virus, become infected when they feed on grass contaminated by bat urine. Humans are then infected through contact with the horses (Plowright et al., 2015). Replanting trees that produce winter nectar, while protecting existing winter flowering habitats, will allow bats to feed away from agricultural areas, reducing the risk of pathogen spillover. Protected and conserved areas can



Rodents are among the most significant zoonotic pathogen hosts worldwide. Palm squirrel, Hyderabad, India © Jamie Reaser

complement these restoration efforts and amplify large-scale rewilding initiatives that support landscape immunity benefits.

The strategic removal of invasive plants that support populations of zoonotic pathogens, vectors or hosts can also function as an ecological countermeasure (Reaser et al., in press). In Mauritius, invasive alien plants have reduced the habitat quality of the Mauritian Flying Fox (*Pteropus niger*), resulting in increased foraging in agricultural lands and urban environments. Krivek et al. (2020) showed that non-native plant invasions reduced native fruit production and that weeded forests provide a better habitat for Flying Foxes. They conclude that their study lends support to invasive alien plant control as a management strategy in mitigating human–wildlife conflicts.

Japanese Barberry (*Berberis thunbergii*), a woody understory shrub, was introduced to the United States from Asia in 1875 for ornamental landscaping. It is now widespread outside of cultivation, invading natural areas (especially meadows, forest and wetlands) throughout much of the United States and eastern Canada (USDA/NRCS, 2020). Japanese Barberry is worrisome from a zoonotic disease perspective for two reasons: the plant infestations provide microclimates favourable to Blacklegged Ticks, the vector responsible for several human diseases, including Powassan virus and Lyme disease (Williams & Ward, 2010); and they provide nesting areas for White-footed Mice (*Peromyscus leucopus*) and other rodents that function as reservoir hosts (Linkske et al., 2018). Ward et al. (2013) found that the number of Blacklegged Ticks averaged 297 per hectare in barberry-infested forests compared to 25 per hectare in forests without Barberry. Linkske et al. (2018) found that management of Barberry stands reduced contact opportunities between Blacklegged Ticks and White-footed Mice; they encouraged eradication and control of the invasive shrub to reduce the number of *B. burgdorferi*-infected Blacklegged Ticks. The Kestrel Land Trust of Amherst, Massachusetts (USA) has prioritised control of Japanese Barberry on multiple properties under its conservation management with some success in controlling early-stage infestations.[8]

Practice 9: Educate and change human behaviour

Human-driven problems require human-targeted solutions. The effectiveness of measures that address human behaviour depends on an understanding of the prevailing socio-economic factors and how they change over time. Muehlenbein (2016) points out that social scientists must play a central role in understanding differing cultural attitudes towards other species, as well as perceived risks when humans interact with animals. He argues that the management of emerging infectious diseases is best accomplished through human behavioural changes rather than disease surveillance.

Messages that promote the value of wildlife while discouraging contact between humans and wildlife are essential in preventing land use-induced spillover, as well as the conservation of biodiversity in protected and conserved areas. Educational efforts by public health officials that blame people for disease outbreaks and/or fail to instill a value in native wildlife can lead to wildlife culling and the destruction of wildlife habitats.

Social marketing approaches have been used successfully to work with communities to identify and implement the human behaviour changes necessary to support conservation and human health goals, separately and combined (MacDonald et al., 2012). For example, in Bangladesh, Hassan et al. (2020) used a standard knowledge and values survey to understand community perceptions and knowledge of bats as they relate to the transmission of Nipah virus. Their findings enabled them to recommend interventions to raise awareness of the zoonotic disease issues and improve local people’s knowledge and acceptance of the role of bats.

In Sri Lanka, Dittus et al. (2019) used a similar approach to understand the social dynamics associated with human–monkey conflicts. They found that 80 per cent of people surveyed in the local community wanted troublesome monkeys translocated from their properties to protected and conserved areas; an impractical solution: very few (< 1%) wanted them destroyed. They concluded that the combination of a feeding ban, possibly contraceptive intervention at localised conflict spots, and extensive education may provide a benign alternative to the destruction of wild primates favoured by a powerful minority.

Practice 10: Invite interdisciplinary collaborations

Since protected and conserved areas typically provide strong ecological contrasts between non-disturbed core areas and moderate- to highly-disturbed zones at the periphery, they may serve as natural laboratories for studies of land use-induced spillover. Within the One Health and Planetary Health contexts, Plowright et al. (2020) discuss the need for interdisciplinary collaboration to study the environmental stressors that trigger the infect–shed–spill–spread cascade. Protected and conserved area managers can forge collaborations by, for example, facilitating or undertaking:

A. The surveillance of wildlife for pathogens, particularly birds and mammals likely to come into contact with people (e.g., Uhart et al., 2015) (see Practice 2);
B. Cataloguing protected and conserved area species in research accessible databases. Particular effort should be made to document animal species that can act as zoonotic pathogen hosts or vectors, as well as plant species that provide habitat, food or other resources for these animals. Both native and non-native species should be included in the databases (see Plowright et al., (2021) and Reaser et al., (2020b) for relevant discussion);
C. Collection of serum samples from wild host species to characterise wildlife health under various environmental conditions (Demas et al., 2011; Plowright et al., 2019); and
D. Data collection on the behavioural and socio-economic factors that influence wildlife–human proximity (e.g., Dittus et al., 2019) (see Practice 9).

Such work can increase our knowledge of pathogen diversity and distribution, pathogen circulation in wildlife populations, how environmental conditions influence wildlife immune status and infection dynamics, and the drivers of human exposure to zoonotic pathogens. For example, a workshop funded by the Bill and Melinda Gates Foundation in Africa brought mosquito experts together with invasion biologists to discuss the links between invasive alien plants, mosquitoes and associated diseases. The interdisciplinary dialogue identified and facilitated several new paths of research.[9] In Australia, sampling of Pteropodid bats for Hendra virus has been conducted in collaboration with staff managing several protected and conserved areas. Researchers working with staff from the Queensland Department of Natural Resources were able to locate animals during a food shortage and show a relationship between nutritional stress and Hendra virus seropositivity (Plowright et al., 2008).

CONCLUSION

The COVID-19 pandemic has shown the staggering global costs of this zoonotic disease outbreak in human lives and money. As pressures on ecological systems mount around the globe, the next pandemic is already in the making. We know protecting nature benefits human health. We also know that protected and conserved areas can be managed to diminish the risk of land use-induced spillover by fostering landscape immunity and preventing contact between animals that host zoonotic pathogens and people. As far as possible, protected and conserved area managers need to keep systems intact, restore degraded ecosystems and facilitate ecological connectivity. Protected and conserved area managers also need to be attentive and responsive to zoonotic disease risk when integrating the needs of wildlife with those of the human communities that live in and around protected and conserved areas.

Nations can no longer treat conservation as a second order priority. The Post-2020 Global Biodiversity Framework that includes decadal revisions of the Convention on Biological Diversity targets, the United Nations Framework Convention on Climate Change, and aligned multi-lateral environmental agreements must now adopt Post-COVID-19 strategies in their forward-looking agendas, including the aim to place at least 30 per cent of the world in protected and conserved areas by 2030.[10] COVID-19 shows that – as part of these strategies – we should now recognise that protected and conserved areas are at the frontline of public health infrastructure and that their managers are vital to disease prevention. It is now readily apparent that investments in protected and conserved areas are investments in humanity. Looking ahead, we have to conserve nature as if our lives depended on it.

ENDNOTES

[1]Although zoonotic pathogens have been documented across a diversity of ecosystems, this paper largely focuses on terrestrial and freshwater environments. This reflects the greater depth of knowledge and risks associated with these systems, as well as

the disciplinary expertise of the authors. We encourage greater attention to zoonotic pathogen dynamics in marine environments.

[2]http://www.glews.net/, accessed 12 November 2020

[3]Guidelines for Assessing the Risk of Non-native Animals Becoming Invasive: https://www.oie.int/fileadmin/Home/eng/Our_scientific_expertise/docs/pdf/OIEGuidelines_NonNativeAnimals_2012.pdf, accessed 12 November 2020

[4]https://www.usaid.gov/ept2, accessed 12 November 2020

[5]For example: http://www.batonehealth.org, accessed 12 November 2020

[6]The points made is this paragraph are also applicable to fragment size (Practice 4A)

[7]https://ugaticks.weebly.com/, accessed 12 November 2020

[8]https://www.kestreltrust.org/controlling-invasive-plants-6-2019/, accessed 12 November 2020

[9]A. Witt, pers. com. Held at Lake Naivasha, near Nairobi, Kenya under CABI contract CPT009350

[10]https://www.cbd.int/doc/c/efb0/1f84/a892b98d2982a829962b6371/wg2020-02-03-en.pdf, accessed 12 November 2020

[11]https://www.cabi.org/about-cabi/who-we-work-with/key-donors/, accessed 12 November 2020

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ABOUT THE AUTHORS

Jamie K. Reaser is President of Giving Voice to Resilience and adjunct faculty at George Mason University. https://orcid.org/0000-0003-3879-0100

Gary M. Tabor is President of the Center for Large Landscape Conservation and Chair, IUCN/WCPA Connectivity Conservation Specialist Group https://orcid.org/0000-0003-4711-1018

Daniel J. Becker is an assistant professor at the University of Oklahoma. https://orcid.org/0000-0003-4315-8628

Philip Muruthi is Vice President for Species Conservation and Science at the African Wildlife Foundation.

Arne Witt is CABI's Regional Coordinator (Africa and Asia) for Invasive Alien Species. https://orcid.org/0000-0003-2257-4411

Stephen J. Woodley is Vice-Chair for Science and Biodiversity with IUCN's World Commission on Protected Areas. https://orchid.org/0000-0003-3074-6578

Manuel Ruiz-Aravena is a postdoctoral researcher at Montana State University (USA). https://orcid.org/0000-0001-8463-7858

Jonathan A. Patz is Professor and John P. Holton Chair of Health and the Environment at the University of Wisconsin-Madison. https://orchid.org/0000-0002-7131-9698

Valerie Hickey is an environmental scientist working at the World Bank Group.

Peter J. Hudson is the Willaman Professor of Biology at Penn State University. https://orcid.org/0000-0003-0468-3403

Harvey Locke is co-founder and strategic advisor of the Yellowstone to Yukon Conservation Initiative and Chair of the IUCN World Commission on Protected Areas Beyond the Aichi Targets Task Force. https://orcid.org/0000-0003-3882-5852

Raina K. Plowright is an associate professor of epidemiology at Montana State University. https://orcid.org/0000-0002-3338-6590

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RESUMEN

Los sistemas terrestres están sometidos a una presión cada vez mayor debido a la expansión de la población humana y la intensificación del uso de los recursos naturales. En consecuencia, los microorganismos que causan enfermedades están surgiendo a medida que la dinámica de los patógenos en la fauna silvestre se ve alterada por el cambio de uso de la tierra, propiciando un mayor contacto entre la fauna silvestre y las personas. Ofrecemos una breve visión general de los procesos que rigen las “repercusiones inducidas por el uso de la tierra”, haciendo hincapié en las condiciones ecológicas que fomentan la “inmunidad del paisaje” y reducen la probabilidad de que la fauna silvestre que alberga los patógenos entre en contacto con las personas. Si los ecosistemas permanecen saludables, es más probable que la vida silvestre y las personas también lo hagan. Recomendamos diez prácticas para reducir el riesgo de futuras pandemias mediante la gestión de áreas protegidas y conservadas. Nuestras propuestas refuerzan las estrategias de conservación existentes, elevando al mismo tiempo la conservación de la biodiversidad como medida sanitaria prioritaria. La prevención de pandemias subraya la necesidad de considerar la salud humana como un servicio de los ecosistemas. Hacemos un llamamiento para que los marcos de conservación multilaterales reconozcan que los administradores de áreas protegidas y conservadas están en la primera línea de la seguridad y salud públicas.

RÉSUMÉ

Les systèmes terrestres subissent de plus en plus de pressions en raison de l'expansion de la population humaine et de l'intensification de l'utilisation des ressources naturelles. Par conséquent, les micro-organismes qui causent des maladies émergent à mesure que la dynamique des agents pathogènes dans la faune est modifiée par le changement d'utilisation des terres, mettant davantage en contact la faune et les personnes. Nous donnons un bref aperçu des processus régissant les «conséquences induites par l’utilisation des terres» et mettons l’accent sur les conditions écologiques qui favorisent «l’immunité du paysage», réduisant ainsi la probabilité que la faune qui héberge des agents pathogènes n’entre en contact avec les humains. Si les écosystèmes restent sains, cela sera le cas pour la faune et les humains également. Nous recommandons dix pratiques pour réduire le risque de futures pandémies grâce à la gestion des aires protégées et conservées. Nos propositions renforcent les stratégies de conservation existantes tout en faisant de la conservation de la biodiversité une mesure sanitaire prioritaire. La prévention de la pandémie souligne la nécessité de considérer la santé humaine comme un service écosystémique. Nous appelons les cadres de conservation multilatéraux à reconnaître que les gestionnaires d'aires protégées et conservées se trouvent en première ligne pour la protection de la santé publique.