Deploying Ecological Countermeasures as a Biosecurity Imperative

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Abstract

The COVID-19 pandemic has brought biosecurity to the forefront of national security policy. Land use change is a fundamental driver of zoonotic disease outbreaks, yet substantial study is yet required to unravel the mechanisms by which *land use-induced spillover* operates. Ecological degradation may be the 21st Century's most overlooked security threat. Within the biosecurity context, we introduce ecological countermeasures as highly targeted, landscape-based interventions aimed at arresting one or more of the components of land use-induced spillover, the chain of biological events that facilitate large-scale outbreaks of diseases transmitted between wildlife and people. We provide case studies of ecological countermeasures of particular interest to the US Department of Defense, broadly discuss countermeasures in the defense and health sectors, and provide an overview of recent US policy decisions related to health security in order to underscore the need for greater attention to ecological resilience as our best defense against future pandemics.

Key words: biosecurity**,** ecological countermeasures, land use-induced spillover, pathogen spillover, zoonotic disease

Environmental and human health are core contributors to national security (National Academy of Sciences 2017). For decades, there have been calls for governments to take a more comprehensive approach to biosecurity as a component of national security (e.g., Meyerson et al. 2009, Koblentz 2010). We define *biosecurity* for the purposes of this paper as measures aimed at preventing the introduction and spread of biological organisms harmful to human assets, including lives and livelihoods. In the United States, policy actions are increasingly consistent with the premise that a wide range of biologically-based threats place the nation at risk. This is evidenced in recent executive actions, including policies that explicitly place health security and biological preparedness in the national security context (Executive Office of the President [EOP] 2021c); connect human, animal, and environmental health within the Global Health Security Strategy (Michaud et al. 2019); and frame the invasive species issue as a national security imperative (EOP 2016). However, a recent review by the Council on Strategic Risks (Schoonover et al. 2021) states that "global ecological disruption is arguably the 21st Century's most underappreciated security risk" and that "both climate and broader ecological security risks continue to be under-recognized as issues with present and tangible consequences for safety, security, and US strategic interests."

The COVID-19 pandemic has rapidly brought biosecurity to the forefront of policy making worldwide, drawing civil society's attention to the implications of "wildlife diseases" on human populations. More than 75% of emerging zoonoses, infectious diseases that are transmitted from animals to humans, have been initially detected in wildlife (Jones et al. 2008). While pathogens are a fundamental aspect of ecological systems, various perturbations can disrupt the dynamics that govern pathogen-wildlife interaction. Typically, land use change is the primary trigger for the chain of events by which zoonotic pathogens pass from wildlife to humans (Gottdenker et al. 2014, Hassell et al. 2017; White and Razgour 2020). This process includes: a) free-living wildlife becoming infected with pathogens (i.e., contracting disease; becoming a pathogen *host*), b) the infected host shedding viable pathogens into the environment (e.g., via feces, urine, saliva), c) human exposure to the pathogens with subsequent infection (i.e., spillover; Plowright et al. 2017), and d) further spread of the pathogen through the human population (Lloyd-Smith et al. 2009, Wasik et al. 2019). Once pathogens have *spilled over*, subsequent transmission from human to human may result in a small number of cases (clusters), or may lead to regional (epidemic) or global (pandemic) outbreaks, a phenomenon known as an *emergence*. Plowright et al. (2021; Figures 1 and 2 therein) described this infect-shed-spill-spread cascade in the context of altered ecological conditions, terming it *land use-induced spillover*.

Wildlife consumption and trade are closely tied to land use changes; impacts on natural resources may force local people to find alternative ways to sustain themselves and habitat degradation often enables greater access to wildlife. Wildlife consumption and commerce are thus important factors to address in order to reduce the risk of human exposure to zoonotic pathogens (Can et al. 2019, Kolby 2020). However, the most fundamental approach to preventing future pandemics is to investigate and arrest the ecological conditions that initiate land use-induced spillover (Plowright et al. 2021). This biosecurity could be achieved by: a) fostering *landscape immunity*, the ecological conditions that, in combination, keep pathogen populations in check and foster the immunological defenses of wildlife within a specific ecosystem, and b) minimizing the risk of human exposure to zoonotic pathogens, which we refer to as managing the *dynamics of wildlife-human proximity* (Reaser et al. 2020a, 2021a). Here, we introduce *ecological countermeasures* as a technical approach to achieving biosecurity at the landscape scale, making the case that national security is much more than a border control issue. We believe that it is time to consider how the condition of lands and waters impact global health security and recognize that our best defense against future pandemics is ecological protection and restoration—measures that will enable ecological systems to be more resilient to acute and chronic perturbations.

Ecological countermeasures defined

Ecological countermeasures are highly targeted, landscape-based interventions aimed at arresting one or more of the components of land use-induced spillover. Reaser et al. (2021b) recently framed this concept as an aspect of ecological restoration intended to achieve resilience to anthropogenic disturbances at the ecosystem scale. We place ecological countermeasures squarely within the biosecurity context, with emphasis on the defense and health sectors; provide examples of ecological countermeasures of interest to the United States (US) Department of Defense (DOD); and emphasize the importance of ecological countermeasures in building a more biologically-informed approach to national security. Ecological countermeasures are biosecurity measures that warrant at least as much research and development investment as other technical approaches to zoonotic disease risk reduction (e.g., vaccines, vector biocontrols; see Sokolow et al. 2019, Figure 1). Without question, spillover prevention is the most cost-efficient approach to future policy development (Dobson et al. 2020). We believe it is also the most ethical way forward.

From an environmental perspective, *countermeasures* typically refer to site remediation and restoration activities undertaken to address contaminants (e.g., Fesenko and Howard 2012, Shuangchen et al. 2017). The ecological countermeasures concept and term arose out of a DOD Defense Advanced Research Projects Agency (DARPA) supported project focused on the dynamics of henipavirus spillover from flying foxes (fruit bats; *Pteropus* spp.) to humans in Asia, Africa, and Australia (Plowright DARPA PREEMPT program cooperative agreement D18AC00031, Figure 2). DARPA's support for the project reflects DOD's acknowledgment that a) more military personnel have died of infectious disease than wounds inflicted in battle (Crillo 2008; *Disease Non-Battle Injury*); b) the risk to the military from infectious diseases affects worldwide geographies to which US personnel may be deployed to support US interests and alliances; c) US military missions, which extend well beyond conflict engagement, include strong commitments to support humanitarian assistance and disaster management programs; and d) outbreaks of infectious disease can drive human suffering and conflict on large scales and can de-stabilize nation states or regions (Connolly and Heyman 2002). Thus, zoonotic disease prevention reduces the need for military intervention and safeguards troops when military action is deemed necessary.

Ecological countermeasure case studies

In the context of henipaviruses and spillover, ecological countermeasures specifically refer to a landscape-based approach aimed at reducing the risk of Hendra virus spillover in eastern Australia. The work is intended to identify and understand the specific processes that lead to spillover such that countermeasures can be developed; and also to provide a clear framework allowing for the development of a generalizable model of how ecological countermeasures can stop spillover of other bat-borne viruses including SARS-like coronaviruses, Nipah, Ebola, and Marburg viruses. Hendra virus is a subtropical and tropical fruit bat-borne virus associated with high fatality in horses (horses acting as a bridging host) and also in humans. It was first isolated in 1994, from an outbreak involving 21 horses and two humans in the Brisbane suburb of Hendra, Australia (Murray et al. 1995, Tulsiani et al. 2011, Plowright et al. 2015). The risk of Hendra virus infection in horses and humans has dramatically increased as a result of the destruction of the native forests that historically provided winter feeding sites for the black flying fox (*Pteropus alecto*) and grey-headed flying fox (*Pteropus* poliocephalus) bat populations. Starting with European settlement, the *Eucalyptus* species that reliably provided winter nectar resources for fruit bats, among a community of other species, have been steadily cleared for large scale agriculture development, and these deforestation rates continue to be some of the highest in the world (Catterall et al. 1998, Bradshaw 2012). The loss of winter nectar (a key ecological service in this forest ecosystem) is an environmentally-induced stressor of bats (e.g., via poor nutrition) that triggers the infect-shed-spill-spread chain of events that leads to Hendra virus spillover (Plowright et al. 2015) through at least two mechanisms: 1) increased viral shedding by bats and 2) increased bat proximity to horses and people inhabiting agricultural areas. Historically, flying foxes were nomadic across vast expanses of their native habitats, moving thousands of kilometers in accordance with tree phenology, often in response to major climatic events. However, winter food shortages have caused these flying foxes to take up residence in human-dominated landscapes where they access reliable but poor-quality foods such as trees planted for decoration, shade, or fruit production. The agricultural landscapes which are new homes for these bats include pastures in which horses may be exposed to bat excrement near the trees upon which the bats feed. Bats from these new flying fox roosts are responsible for almost all Hendra virus spillover events in Australia (Plowright et al. 2011, 2015).

An ecological countermeasure for Hendra virus in this system would need to address the ecological conditions that influence viral shedding and the dynamics of wildlife-human proximity. The ideal solution will not be reached by culling bats, managing horse locality, addressing the technical and social challenges of vaccinating horses (Middleton et al. 2014), or implementing other interventions in the agricultural landscape; the problem is best addressed at its source. An ecological countermeasure is under development with the goal of re-establishing hundreds of hectares of winter-flowering *Eucalyptus* tree species to enable bats to return to a context that conveys landscape immunity (Peggy Eby, University of New South Wales, Kensington, Australia, personal communication, 7 March 2021). This enhanced winter habitat would change the dynamics of human-bat proximity by reducing bat contact with horses, as well as improve the nutritional status of bats, thereby improving immune capacity of the bats resulting in decreased viral shedding (e.g., via urination) of zoonotic viruses (Plowright et al. 2015, 2016, Kessler et al. 2018). Recent observations have provided some proof of concept; biologists have observed that when rich flushes of winter nectar occur, bats leave agricultural roosting sites *en masse* and fly long distances to feed in what remains of their traditional forested landscapes (Peggy Eby, University of New South Wales, Kensington, Australia, personal communication, 7 March 2021).

Tick-borne diseases, such as Lyme disease (Kugeler et al. 2015), are a significant concern for military personnel in the United States and abroad, primarily because the adverse impacts on the health and well-being of military troops, dogs, and horses undermine military readiness. However, tick-borne diseases can also impact everyone who trains in or otherwise uses the nearly 26.9 million acres of land owned, leased, or otherwise possessed by DOD for installations and other facilities. In addition to active-duty members, this may include civil servants, contractors, foreign nationals, military families, and recreationalists, as well as pets and livestock. For these reasons, in 2018, the DOD Office of the Secretary of Defense reached out to the National Invasive Species Council (NISC) to request support from its associated Invasive Species Advisory Committee (ISAC) in obtaining expert recommendations for risk mitigation (Supplement S1). ISAC (2019) responded via a white paper suggesting: 1) adoption of a “One Health” approach that integrates environmental, animal, and human health considerations; 2) establishment of an inter-agency information sharing network; and 3) routine contact at the facilities-level with experts in on-the-ground risk mitigation. With regard to the latter, the authors noted that invasive plants, such as Japanese barberry (*Berberis thunbergii*) which has become widespread throughout the United States since imported from Asia in 1875 for ornamental landscaping (https://plants.usda.gov/core/profile?symbol=BETH, accessed 4 February 2021), are known to foster ideal habitat for high-risk, disease-vector ticks (e.g., blacklegged tick, *Ixodes scapularis*) while also providing abundant vegetation for white-tailed deer (*Odocoileus virginianus*) and critical amplifiers of the infection such as white-footed mice, (*Peromyscus leucopus*) can exacerbate the spread of disease (Williams and Ward 2010, Linske et al. 2018). It also noted that an understanding of which invasive species have the greatest impact on the density of pathogen vectors, or the likelihood of facilitating ticks contact with wild or domestic host species, could enable managers to prioritize invasive species management activities, especially when resources and personnel are limited.

ISAC was stating that plant invasion can drive land use-induced spillover and that it could be mitigated by managing invasive plants so as to recover landscape immunity and address the dynamics of proximity between humans and pathogen-vectoring hosts. Reaser et al. (2021b; Figure 1 therein) proposed Japanese barberry eradication as an ecological countermeasure, citing barberry removal experiments in which Williams and Ward (2010) found that intact barberry stands had 280 ± 51 adult blacklegged ticks/ha, which was significantly higher than for controlled (121 ± 17/ha) and no barberry (30 ± 10/ha) areas. Further, Linske et al. (2018) found that management of barberry stands reduced contact opportunities between blacklegged ticks and white-footed mice. They encouraged the eradication and control of the invasive shrub to reduce the number of *B. burgdorferi*-infected blacklegged ticks. Although Reaser et al. (2021b) is the first to frame the removal of invasive plants as a strategic ecological countermeasure , success in the management of invasive vegetation to reduce vector-borne infections has been acknowledged for decades. Hudson (1986) showed that removal of invasive bracken greatly reduced survival of the tick *Ixodes ricnus,* as well as infection rates of a tick-borne encephalitis variant known as louping ill virus. The DOD may thus be well-motivated and positioned to be the first to devise and demonstrate large-scale ecological countermeasures on lands managed by the US government. The DOD installation estate already plays a critical role in endangered species conservation efforts in the United States. Recent investments in Sentinel landscapes (https://sentinellandscapes.org/, accessed 12 February 2021) that support installation readiness and biodiversity conservation on military bases offer opportunities for future countermeasure efforts.

Countermeasures in the defense sector

In addition to supporting military training and operations on the lands it manages, the DOD is charged with taking the conservation actions necessary to "sustain the long-term ecological integrity of the resource base and the ecosystem services it provides" (CRS 2020, Figure 3). DOD recognizes that environmental and human health are irrevocably linked and thus military personnel are at risk when they occupy degraded environments, and may place others at risk if they spread pathogens or their vectors when relocating (ISAC 2019). The Armed Forces Pest Management Board exists to ensure that environmentally sound and effective programs are in place to prevent invasive species, including pathogens and disease vectors, from adversely affecting DOD operations (https://www.acq.osd.mil/eie/afpmb/; accessed 12 July 2020). Innovative conservation- and human health-relevant research and development is executed through multiple DOD agencies, as well as facilitated by several grantmaking programs, in addition to DARPA (Abraham et al. 2014, NISC 2016).

Military leadership in the environmental conservation and human health agendas may surprise a large portion of the world populace; the public has greater visibility of the adverse impacts of military conflict on the environment and public safety than it does on military interest in protecting human and environmental health. As a result, there is large geographical variation in the way the general public relates to military terms. In much of Europe, Asia, and Australia military goals and environmental protection are largely considered distinct, potentially opposing, agendas. Socio-politically, this has engendered mistrust between the environmental movements and the actions of the military. However, in the Western Hemisphere, military leadership on environmental issues is more commonly institutionalized within defense agency operations and calls for a more unified definition of and comprehensive approach to biosecurity (e.g., Meyerson and Reaser 2002a,b) may facilitate greater alignment in the future.

The concept and practice of ecological countermeasures is thus consistent with the military mission-space, at least within the United States. The term *ecological countermeasure* is also in alignment with military linguistic frameworks. DOD defines *countermeasure* to mean "that form of military science that, by employment of devices and/or techniques, has its object the impairment of the operational effectiveness of enemy activity" (DOD 2020). This definition recognizes countermeasures as a body of science, rather than a single intervention, that applies a diverse array of technical tools and approaches for problem resolution—to impede a potentially harmful agent from becoming harmful. It, therefore, reasons that ecological countermeasures, like any other form of countermeasure, should be applied to security as well as the notion of landscape immunity, an ecological condition that minimizes the risk of zoonotic spillover—*spillover* being the "enemy activity" to be prevented.

Given the origin of the term *ecological countermeasure* it can be linguistically regarded as a military metaphor. Military metaphors have long-been used in the environmental and health sciences, often to convey the need to prevent substantial impact by a presumed adversary. In recent decades, social campaigns have called for policy makers and the public to wage "wars" on hunger, agricultural pests, cancer, drugs, climate change, and human maladies including emerging infectious agents such as Ebola virus and HIV. Of particular relevance here is the work of Larson (2005), Larson et al. (2005), and Janovsky and Larson (2019), that explores the application of military metaphors in efforts to address invasive species, including invasive infectious diseases.

Although Flusberg et al. (2017) found that military metaphors tended to increase the public's willingness to take actions to curb climate change, concern is increasingly being raised that military metaphors are missing the target; actually undermining societal attentiveness and response to critical issues. Two primary reasons for linguistic caution are: a) a misalignment between military constructs and the ecological and physiological processes they are meant to represent, that can facilitate misunderstanding of key principles and b) societal value shifts may be better reflected in language that places people in less-antagonistic, more generative, relationships to the environment and their bodies (Larson et al. 2005, Nie et al. 2016). Sheran (2020) discusses these issues with regard to how public leaders convey their social policies for addressing severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2; the agent of COVID-19 disease).

While we are likewise concerned that over- and mis-use of military metaphors may further dissociate people from the environment and natural processes (i.e. promote biophobia), thus fostering adversarial stances toward the ecological systems of which humans are integral part, we also believe that military metaphors can facilitate advances in conservation and public health when consciously applied in specific contexts with clear, relevant goals. This is consistent with study findings for metaphor application to environmental restoration (Keulatz 2007) and broader public discourse (Fulsberg et al. 2017, 2018). We believe that advancing biosecurity as a core component of national security and raising awareness of the need to regard environmental conservation as a "best defense" strategy are relevant and underemphasized goals within the public policy arena.

Countermeasures in the health sector

In the context of national security, it is also important to note that the term *countermeasure* is already well-established in the health sector and is thus a key concept for integration into the Global Health Security Agenda (https://ghsagenda.org/; accessed 4 February 2021). Medical countermeasures constitute life-saving medicines and medical supplies used to diagnose, prevent, or treat conditions associated with chemical, biological, radiological, or nuclear (CBRN) threats, emerging infectious diseases, or natural disasters (https://www.cdc.gov/cpr/readiness/mcm.html; accessed 4 February 2021). The CDC uses the term *medical countermeasure* (e.g., vaccines, antiviral drugs, antibiotics, and antitoxins) within their public health and emergency preparedness framework (CDC 2008) to guide their capacity to provide medical interventions to targeted population(s) to prevent, mitigate, or treat the adverse health effects of a public health incident. This work is complemented by the US Food and Drug Administration (FDA) Medical Countermeasures Initiative which coordinates medical countermeasure development, preparedness, and response (https://www.fda.gov/emergency-preparedness-and-response/counterterrorism-and-emerging-threats/medical-countermeasures-initiative-mcmi; accessed 4 February 2021). Medical application of *countermeasure* has also been adopted by the World Health Organization (WHO); for example, "sufficiency of countermeasures" is one of the primary criteria the WHO uses to determine if a pathogen is of substantial health risk. Indeed, many zoonotic diseases are considered among the greatest public health threats due to their epidemic potential and countermeasure insufficiencies. (https://www.who.int/activities/prioritizing-diseases-for-research-and-development-in-emergency-contexts; accessed 15 February 2021).

Biosecurity policy development

Biosecurity policy development in the United States has lagged behind that of other counties, most notably Australia and New Zealand (Meyerson and Reaser 2002a, 2003). New Zealand was the earliest adopter of a comprehensive approach to biosecurity; its 1993 Biosecurity Act 1993 (https://www.legislation.govt.nz/act/public/1993/0095/latest/DLM314623.html, accessed 5 February 2021) provides a rigorous framework for preventing harmful organisms from entering the country. New Zealand's strong commitment to enforcing this legislation and the nearly three decades that civil society has had to adopt prevention measures as societal norms undoubtedly played a significant role in the country's ability to rapidly and robustly respond to COVID-19 in a manner that few countries came close to. The country's COVID-related mortality rate (4 per 1 million) is the lowest among the 37 Organization for Economic Cooperation and Development countries (Baker et al. 2020).

In the United States, we cannot identify a national security issue in which there is a greater disparity between the scale of impact and the scale of response than biological invasions, of which non-native zoonotic pathogens are a component. At the Executive Office level, the call for greater comprehensive attention to biosecurity existed within the Carter-era executive order on exotic organisms (EOP 1977) and has since been repeated in two executive orders on invasive species in which NISC was established and then expanded to institute a cost-efficient, cooperative approach to the issue (EOP 1999, 2016). NISC includes the Secretaries of DOD and

HHS, as well as the senior-most leadership of ten other agencies and four components of the EOP. NISC management plans and other guidance documents (https://www.doi.gov/invasivespecies/guidance-documents, accessed 5 February) have placed a strong emphasis on prevention measures, but almost exclusively from the border control perspective. Recently, a more comprehensive vision was reflected in a Special Issue of *Biological Invasions* that responds to NISC's 2016-2018 management plan (Meyerson and Simberloff 2020). For example, Burgos-Rodríguez and Burgiel (2020) reviewed the patchwork of US authorities that unevenly address various aspects of the federal government's legislative capacity to rapidly detect and respond to infectious pathogens, non-native pathogen hosts, and all other invasive species with a view toward addressing framework gaps. Considering the recommendations arising out all of the papers in the special issue, Reaser (2020b) drafted a comprehensive blueprint that outlines policies, goals, and actions to be taken by relevant Executive Branch agencies and components of the EOP to institute a national biosecurity program that engages agencies with missions ranging from border control and defense to human health and conservation. The role of land management agencies in biosecurity is readily apparent. We believe that ecological countermeasures should be a core component of this framework; re-establishing landscape immunity following environmental perturbations and managing wildlife-human dynamics of proximity will minimize the risk of biological invasion by all non-native taxa. This is critically important given the role that a wide range of invasive plants, insects, arthropods, and vertebrates play in amplifying zoonotic disease risks (Chinchio et al. 2020, Ostfeld and Keesing 2020). However, it remains to be seen if the blueprint will influence federal policy making.

The Biden Administration has thus far demonstrated decisive action to address pandemic risks and inter-related national security agendas (https://www.federalregister.gov/presidential-documents/executive-orders/joe-biden/2021, accessed 5 February 2021). The President recently stated that "it is essential that we refresh and reinvigorate our national science and technology strategy to set us on a strong course for the *next* 75 years, so that our children and grandchildren may inhabit a healthier, safer, more just, peaceful, and prosperous world. This effort will require us to bring together our brightest minds across academia, medicine, industry, and government—breaking down the barriers that too often limit our vision and our progress, and prioritizing the needs, interests, fears, and aspirations of the American people" (Biden 2021). This speaks well to biosecurity having an unprecedented priority in the US national security agenda. Yet, there is good reason to urgently draw attention to what remains lacking; an ecological (landscape-based) approach to addressing zoonotic disease is still largely absent from these policy constructs. For example, the National Strategy for COVID-19 Response and Pandemic Preparedness (EOP 2021e) is focused on medical countermeasures and safeguarding the economy. Although it does include a goal to restore US leadership and build better preparedness for future threats, measures to safeguard ecological resilience (landscape immunity) is noticeably absent from a list of measures to "build better biopreparedness and expand resilience for biological threats", which includes monitoring current and emerging biological threats, securing funding to improve biopreparedness, establishing a National Center for Epidemic Forecasting and Outbreak Analytics, and developing a sustainable US infrastructure for biological and pandemic events. Neither the executive order to mobilize the US response to COVID-19 and provide leadership on global health security (EOP 2021a), nor the executive order to protect public health and the environment, as well as restore science to tackle the climate crisis (EOP 2021b), point to the critical role of ecological systems in addressing these issues or direct agencies to take supportive, ecologically-based actions. Even within an executive order focused on the climate crises (EOP 2021d), the only explicit directive focused on ecological resilience is an echoing of the widely-popularized “30 x 30 Goal” which calls for saving at least 30% of US land and water by 2030. Across the full suite of pandemic-related executive actions, we also note the tendency to place agencies such as the Department of the Interior, which has a mission to conserve and manage the nation's natural resources, at the leadership periphery.

An understanding of land use-induced spillover and the deployment of ecological countermeasures are critical to future biosecurity policy development within the United States and abroad. Protecting ecological systems goes far beyond values in aesthetics, outdoor recreation, and long-term access to the natural resources that support the human enterprise. The protection of human health is an ecological service. COVID-19 has aptly demonstrated that site specific measures to maintain and restore landscape immunity should be regarded as biosecurity measures of national priority and global-scale importance. Our assertion is consistent with the “8 pillars of action” that the Council on Strategic Risks proposes to address the security implications of ecological disruption, particularly Pillar 2 to “promote methods that protect and expand critical systems and services”, Pillar 5 to “reduce pandemic risk at point of origin”, Pillar 6 to “amplify ecological and national security issues in the US government”, and Pillar 7 to “initiate an ecological security research agenda” (Schoonover et al. 2021). It is our hope that future actions spurred by the Council’s findings and recommendations will explicitly incorporate ecological countermeasures in policy and practice.

Conclusions

The large-scale protection and restoration of natural systems affords adaption and resilience capacity—what literally enables Earth to sustain humans and all other species. A healthy biosphere is generative in the face of tremendous pressures, including crises that facilitate human conflicts. All of the options and opportunities that humans will have available to them as the world changes in unpredictable and unprecedented ways are ecologically-based. In the context of zoonotic disease outbreaks, ecological countermeasures should be considered fundamental components of the national security arsenal. The performance standards for ecological countermeasures developed by Reaser et al. (2021b) consist with restoration ecology principles could be adopted as standards of federal land management.

In conclusion, we therefore underscore the importance of furthering ecological countermeasures in concept and by term to help normalize zoonotic disease risk management as a core component of national security and emphasize the importance of prioritizing ecologically-oriented concerns and solutions among competing policy issues. Furthermore, it is our hope that frameworks and terms that explicitly make the connection between national security and its ecological foundations will help government administrations increase the support of senior-level representatives from the life sciences within national security bodies and as external advisors. Until this becomes standard practice, governments will not be able to effectively address the threats to ecological systems that subsequently drive the need for humanitarian and military interventions. Ecological resilience really is our best defense.

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Figure, Photos, and Supplemental Materials

Figure 1. Land use-induced spillover

For an animal-origin pathogen to result in a human epidemic or pandemic, an animal must be infected with a pathogen, shed live pathogen in sufficient quantities and circumstances for spillover to susceptible humans—either directly or through intermediary animals or vectors. The pathogen must then sustain human-to-human transmission. Land use change can trigger and further facilitate this infect-shed-spill-spread cascade by, for example, increasing pathogen prevalence, compromising wildlife immune systems via stressful environmental conditions, and increasing contact—direct and indirect—between wildlife and people. The spillover process is complex and will vary according to pathogen and context. Some spillover events lead to pathogen infection and disease outbreaks with extensive onward transmission (e.g., SARS CoV, H1N1 2009 pandemic influenza), facilitating epidemics (local/regional spread) and pandemics (global spread); while others exhibit stuttering (punctuated) transmission (e.g., Nipah virus, monkeypox); or do not transmit through the human population (e.g., rabies, Hendra virus). A better understanding of how land use change influences each of the components of the zoonotic spillover cascade *in situ* will, ideally, enable us to identify and deploy ecological countermeasures for high-risk pathogens/contexts. In addition to protecting human health, ecological countermeasures could benefit wildlife conservation and animal welfare by precluding the wildlife culling and domestic animal euthanasia (which also has economic and livelihood impacts).

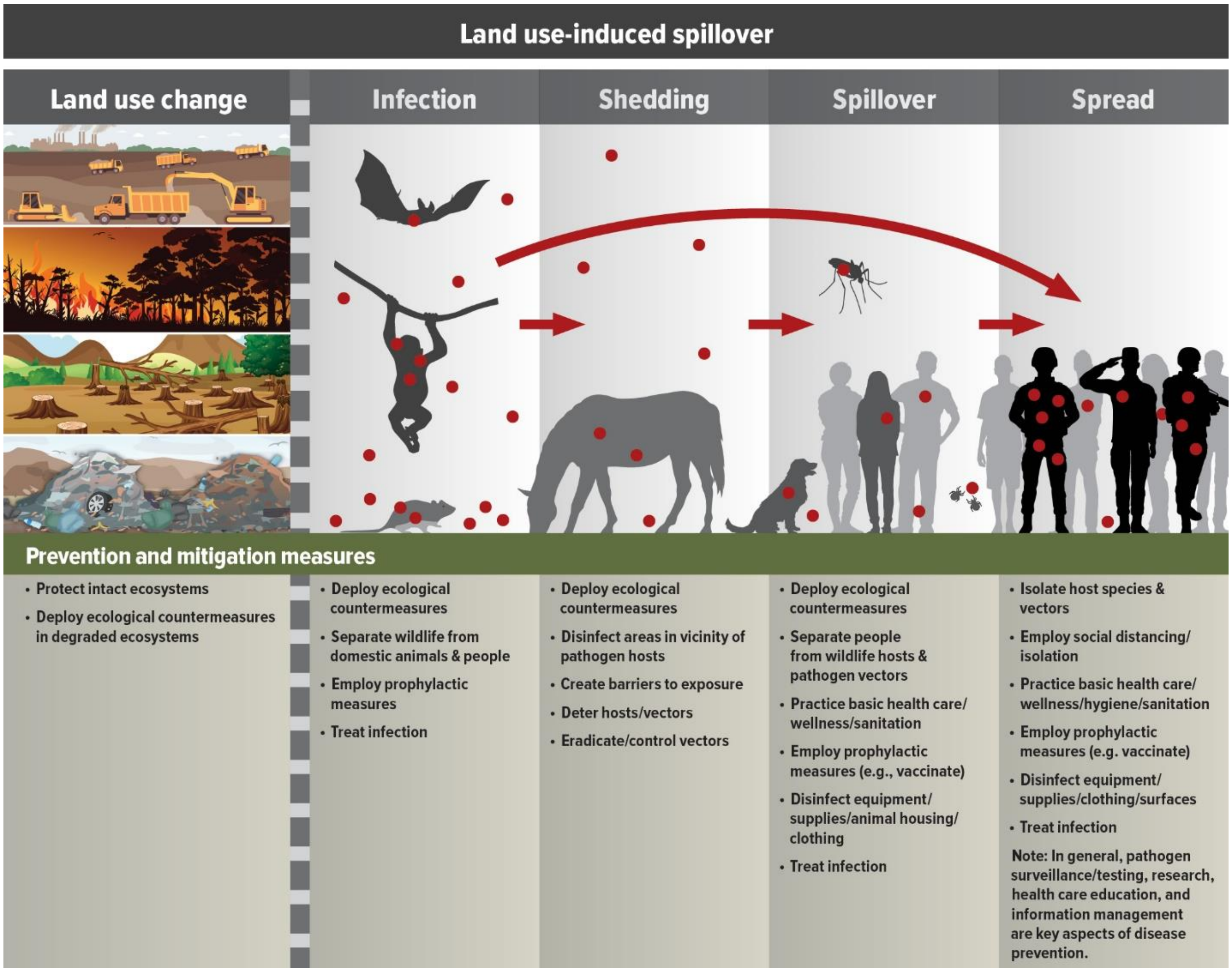
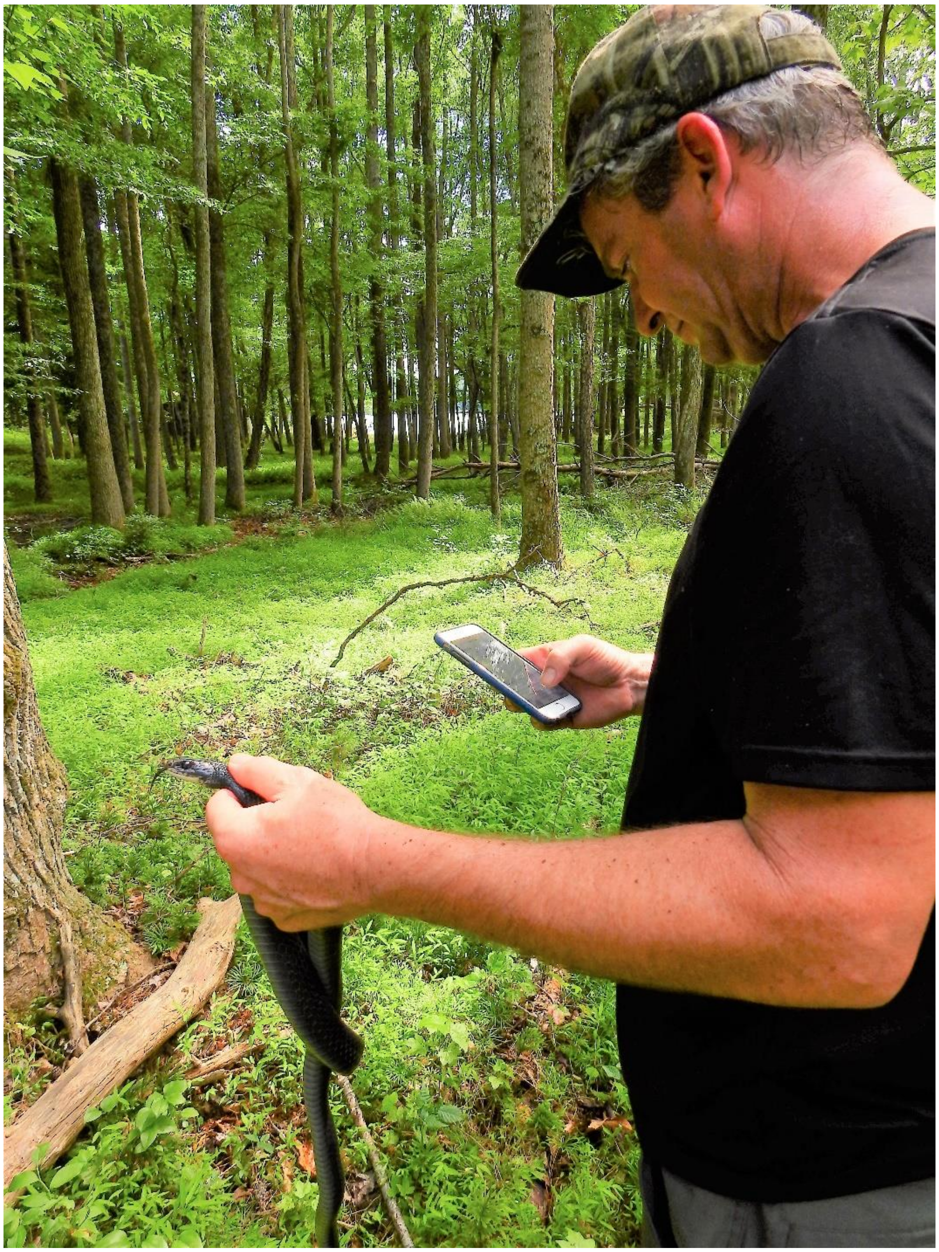

Land use-induced spillover
Land use change
Infection
Shedding
Spillover
Spread
Prevention and mitigation measures
• Protect intact ecosystems
• Deploy ecological countermeasures in degraded ecosystems
• Deploy ecological countermeasures
• Separate wildlife from domestic animals & people
• Employ prophylactic measures
• Treat infection
• Deploy ecological countermeasures
• Disinfect areas in vicinity of pathogen hosts
• Create barriers to exposure
• Deter hosts/vectors
• Eradicate/control vectors
• Deploy ecological countermeasures
• Separate people from wildlife hosts & pathogen vectors
• Practice basic health care/ wellness/sanitation
• Employ prophylactic measures (e.g., vaccinate)
• Disinfect equipment/ supplies/animal housing/ clothing
• Treat infection
• Isolate host species & vectors
• Employ social distancing/ isolation
• Practice basic health care/ wellness/hygiene/sanitation
• Employ prophylactic measures (e.g. vaccinate)
• Disinfect equipment/ supplies/clothing/surfaces
• Treat infection
Note: In general, pathogen surveillance/testing, research, health care education, and information management are key aspects of disease prevention.

Figure 2. Indian fly fox.

Ecological countermeasures are needed to reduce the risk of highly fatal Nipah virus spillover from Indian flying fox (*Pteropus medius*) to humans in Bangladesh. Photo credit: Peter J. Hudson.

Figure 3. Biological survey on military lands

The U.S. Department of Defense's (DOD) mission includes biodiversity conservation. Dr. Robert Lovich, DOD herpetologist and a Senior Natural Resource Specialist for the U.S. Navy, records data on a northern black racer (*Coluber constrictor constrictor*) that he captured during a biological survey at Marine Corps Base Quantico (Virginia, USA). Photo credit: Jamie K. Reaser



Cover photo. Indian flying fox at rest.

The Indian flying fox (*Pteropus medius*) it the reservoir for Nipah virus in Bangladesh. Photo credit: Peter J. Hudson.

Supplement 1 (S1): Letter from the Department of Defense (DOD) to the National Invasive Species Council (NISC), 1 November 2018; officially transmitted to co-author Jamie K. Reaser.

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