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Pandemics and the human-wildlife interface in Asia: land use change as a driver of zoonotic viral outbreaks

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Abstract

Pandemics have occurred with increasing frequency over the past century as global travel enables rapid cross-continental transmission of viral zoonoses such as coronaviruses and influenzas. Yet the prevalence of global pandemics is also attributable to an increase in the number of these infectious diseases originating in wildlife or domesticated animals in Asia that jump to human hosts. Through a review of scholarly literature, this article argues that three interrelated land use phenomena—biodiversity loss, urbanization, agricultural expansion and intensification—in southern China and Southeast Asia have enabled past viral zoonotic 'spillover' events from animals to humans and make future pandemics more likely. Furthermore, much recent scholarly literature on zoonotic disease adopts the One Health framework, which highlights interdependency between viruses, animals, ecosystems, and human health. As such, we review and critique the salience of the One Health framework for research on zoonotic disease in Asia. We suggest that to better understand land use changes enabling zoonotic disease emergence, future health-environment research could incorporate qualitative, cross-scalar political-economic and political ecological dynamics within which human-wildlife relations are embedded.

1. Introduction

The majority of viral outbreaks that have led to pandemics over the past century share two common dynamics: they are zoonotic influenza viruses or coronaviruses that 'jumped' from animals to humans, and they first emerged in Southeast Asia (SEA) and southern China⁴. Prior to the 2019 emergence of SARS-CoV-19 (COVID-19) in Wuhan, China, zoonotic viral outbreaks that began in the region include the 1918 Spanish flu thought to have originated in China, the Asian flu in southern China in 1957, the H3N2 influenza in Hong Kong in 1968, Nipah (NiV) virus in Malaysia in 1999, SARS in southern China in 2002, and H5N1 avian influenza in Hong Kong in the early 2000s (Curley and Thomas 2004, Walsh 2015, Mostafa et al 2018)⁵. While Asia is certainly not the only region in which zoonotic viral outbreaks have originated (human immunodeficiency virus (HIV) and Ebola being notable exceptions that first emerged in Africa) conditions in both mainland SEA (Vietnam, Laos, Cambodia, Thailand, Myanmar, and Malaysia), maritime SEA (Indonesia, Philippines, and Malaysia), and southern China nevertheless favor the emergence of new zoonotic pathogens and facilitate the persistence of endemic zoonoses. Extensive mammalian biodiversity, circular rural-urban migration, widespread regional trade, increasing agricultural industrialization, and tropical and subtropical climate conditions make this Asian

⁴ Exceptions to this include the 2009 H1N1 influenza outbreak, which originated in pigs in Mexico and spread through the United States, and MERS, a coronavirus that originated in Saudi Arabia in 2012; nor does this consider the zoonotic HIV originating in Africa, which the WHO considers a 'global epidemic'.

⁵ Nipah virus has not caused a pandemic to date but outbreaks originating in fruit bats and pigs in Malaysia and India have led the WHO to consider it a potential cause of future pandemics.

region a 'hotspot' for zoonotic viral disease and what Plowright *et al* (2021) refer to as 'land use-induced spillover' (Bordier and Roger 2013, Allen *et al* 2017).

At the most fundamental level, the World Health Organization (WHO) defines zoonoses as pathogens that can be passed between vertebrates (Bordier and Roger 2013). They are transmitted between humans and animals, including wildlife, domesticated livestock, and pets, via either 'spillover' events from excretion and slaughter where wildlife and domestic populations live in proximity or directly to human populations via host or parasite translocation (Fèvre and Grace 2017, Plowright et al 2017). Spillover events are shaped by frequency, duration, and intimacy between hosts and wildlife reservoirs (Rohr et al 2019). Zoonotic diseases are distinct from vector-borne diseases, which are transmitted between vertebrate hosts via an arthropod 'vector' such as mosquitoes (Morens et al 2004, Burkett-Cadena and Vittor 2018)⁶. Roughly 60% of all human diseases are zoonotic, with nearly 20% of those originating in domesticated animals; 75% of all infectious diseases that emerged between 1940 and 2004 are zoonotic (Jones et al 2008, Machalaba and Karesh 2017, Goodin et al 2018, Grace 2019). Though zoonoses can be bacteria, protozoa, fungi, or viruses, this article focuses on influenza and coronaviruses as a source of highly contagious disease outbreaks in humans.

Many outbreaks of zoonotic pathogens over the past two decades have also been described as 'emerging infectious diseases', or EIDs (Leach et al 2021). The term has been applied both to pathogens that were well-identified in previous decades as well as to diseases with new etiologic understandings or geographic distributions (Farmer 2009, Leach and Scoones 2013). EIDs are rarely linked to novel virulence alone; land use changes, including deforestation and urbanization, associated loss of biodiversity, and the industrialization of livestock farming all shape their emergence and transmission (Farmer 2009, Plowright et al 2021). Changes to the built and natural environment will inevitably alter patterns of disease outbreaks and human exposure to them, reflecting inter-dependency between sociopolitical and environmental factors in disease occurrence and human health outcomes (King 2010, Li 2017, Connolly et al 2021, Yang and Lo 2021). Largescale environmental changes alter species and pathogen abundance, exposure rates and types, and drivers of pathogen evolution. Forest conversion and land use change can reduce barriers for the spread of disease and associated economic impacts can be consequential for disease burdens and their impact on human health (Machalaba and Karesh 2017). Humans are responsible for significant ecological

perturbation, habitat fragmentation, and significant shifts in global climate patterns; environmental degradation and related social inequality in turn can increase disease transmission and human vulnerability to infectious disease (Yang et al 2015, Yang and Lo 2021, Sathyamala 2022). For instance, in mainland SEA, forest cover declined 50% from 1998 to 2018, including in protected areas, reflecting extensive expansion of agricultural plantations and natural resource extraction, and leading to biodiversity loss (Sodhi et al 2004, Kenney-Lazar and Ishikawa 2019, Namkhan et al 2021). Yet as Waltner-Toews points out, 'substantive links between those investigating, and responding to, EIDs as products of social, economic and political forces, and those viewing them through biomedical or ecological lenses, have been slow to emerge' (Waltner-Toews 2017, p 2; see also Liverani et al 2013, Murray et al 2016).

One salient question in assessing viral pandemics with zoonotic origin is whether they are emerging more frequently than in the past or whether they are being detected more often. In the case of viruses originating in bats, identification of bat species as probable viral hosts can arguably be attributed to increased surveillance of bats after the initial discovery of antibodies in bat populations. However, targeted surveillance or improved diagnostic capabilities alone cannot adequately explain the emergence of the NiV virus or SARS coronavirus and subsequent major disease outbreaks (Field 2009). In other words, the outbreaks would have still occurred (and likely been identified) but their origins would have remained unknown without surveillance research. The absence of evidence of previously unidentified outbreaks from retrospective examination of a historical case or necropsy data also supports increased emergence over increased detection. Furthermore, in addition to the presence of a viral agent, disease emergence requires an effective bridge between the natural host and the susceptible spillover host (Morens and Fauci 2013). Such bridges are the result of natural or anthropogenic changes to the agent, host, or environment; extensive and rapid anthropogenic changes to hosthost relations and host-environment relations are now common throughout Asia.

In this paper, we present an up-to-date and comprehensive synthesis of academic research on the socio-environmental dynamics of viral zoonotic outbreaks in Asia. Most of this research is focused on the emergence of zoonotic disease, that is, the drivers of possible 'spillover' events at the human-livestockwildlife interface; dynamics that enable widespread human-to-human disease transmission are mentioned in brief but largely remain beyond the scope of this paper. Based on a scoping review of peerreviewed literature that draws on research on and from SEA and southern China, we identified three interrelated factors pertaining to land use change that enable the emergence of viral zoonoses that

⁶ Though some phenomena discussed in this paper are applicable to vector-borne diseases, infectious disease linked to vectors such as mosquitoes is beyond the scope of this article.

cause contagious infectious disease in humans: biodiversity loss, peri-urban development, and agricultural expansion and intensification. We refer to these underlying and proximate political-economic and socio-environmental conditions as drivers or enablers of zoonotic viral outbreaks, rather than causes, which most commonly describes disease occurrence in individuals. Additionally, we offer an overview of scholarly frameworks that have been used to research human-environment dynamics surrounding health, with a focus on the dominant One Health framework and its critiques, plus the parallel development of landscape epidemiology as a field. We suggest that the field of political ecology of health, with its focus on political economy, landscape change, and individual agency, has much to offer future research on the emergence and transmission of non-vector viral zoonoses where One Health has fallen short. This paper thus offers a muchneeded synthesis of literature preceding yet relevant to the COVID-19 pandemic, and understanding of the structural factors that may enable future viral pandemics. While we also acknowledge the important role of non-structural factors, including individual agency, community action, and context-specific contingency, in contributing to zoonotic disease outbreaks and transmission (Senanayake and King 2019, Leach et al 2021), research on those factors remains understudied in our region of concern as determined by our review. This study in no way intends to place blame on communities in Asia for these viral outbreaks while absolving other regions of the world of responsibility: to the contrary, we suggest that a richer analysis of zoonotic disease outbreaks would take cross-scalar and global political-economic drivers of biodiversity loss, land use change, industrial agricultural production, and urbanization into account.

2. Methodology

Our findings are based on literature review methodology and expert knowledge to identify and evaluate the socio-environmental factors that contribute to zoonotic viral disease emergence and transmission in Asia with an emphasis on contagious influenza and coronavirus outbreaks that led, or could have led, to pandemics. Literature selected for this review was found using academic search engines including Web of Science, Scopus, and Science Direct, and the review included articles from journals such as Science, Nature Sustainability, Social Science and Medicine, The Lancet, Philosophical Transactions of the Royal Society B: Biological Sciences, and World Development. We focused on articles with empirical data from or case studies based in Asia, primarily SEA (Indonesia, Vietnam, Singapore, Malaysia, Brunei, Laos, Myanmar, Philippines, and Cambodia) and China. The review began with the identification of key search terms,

listed in table 1. The first phase of the research process involved filtering through different combinations of those key search terms. For the bulk of our search, we aimed at avoiding early findings pertaining to the SARS-CoV-2 pandemic, most of which were nonpeer reviewed commentaries or editorials published in 2020 through early 2021. Results were filtered with a custom date range through December 2021. Quotation marks were applied around each search term such that a search including 'land use' and 'one health' and 'pandemics' and 'Southeast Asia' only returned articles that covered all four search terms.

The search formula returned 189 results. Potential articles for review were first assessed based on title; titles of interest were then reviewed by abstract. Those with findings related to pandemics, zoonotic disease, and human-environment interactions pertaining to land use or wildlife were selected for full review. Our review specified criteria for article exclusion: literature lacking discussions of any humanenvironment interactions (i.e. biomedical articles), articles published in a language other than English, articles without full text available through our university institutions' databases, and articles not peer-reviewed (e.g. published in a non-peer reviewed journal, editorials, or commentaries) were excluded. Reflecting the emphasis of this literature review on socio-environmental dynamics of zoonotic pandemics as well as the authors' social science backgrounds, articles focused on public health or epidemiology were included, but articles written from a strictly clinical or biomedical perspective were excluded. An example of the search process for search combinations starting with column 2 are shown in table 1.

Once articles were collected, full-text reviews were conducted, and key findings were identified and organized according to the following categories: (a) frameworks for understanding zoonoses in human-environment contexts; (b) biodiversity and infectious zoonotic disease; (c) land use change as a driver of viral zoonotic emergence with subcategories (1) urbanization and (2) agricultural expansion and intensification. A supplementary search was conducted for articles that provided conceptual overview of the One Health framework, discuss the disciplinary history of One Health and landscape epidemiology, provided an overview of political ecology of health, and articles drawing on political ecology of health to analyze virus and landscape interactions, which is presented in section 3.

3. Frameworks for understanding zoonoses in human–environment contexts

In a significant departure from biomedical models of health and disease, One Health has popularized analysis of health issues at a global scale and across species by considering ecosystem dynamics,

(Land use) OR		(One health) AND		(Pandemic) AND		(Asia)		(Diseases)	
(a) (b)	Agricultural expansion Deforestation	(a) (b)	Conceptual frameworks Public health	(a) (b)	Diseases Emerging infectious diseases	(a) (b) (c)	Brunei Cambodia China	(a) (b) (c)	NiV H1N1 Avian influenza
(c) (d) (e)	Human– environment Industrial agriculture Sustainable development	(c)	Landscape epidemiology	(c) (d)	Zoonoses Zoonotic diseases	(d) (e) (f) (g) (h) (i)	Indonesia Laos Malaysia Singapore Thailand Philippines	(d) (e)	Coronavirus SARS
(1)	Urbanization					(j) (k)	Vietnam Southeast Asia		

Table 1. Key search terms.

We used Boolean operators, the wildcard technique, and the proximity operator in formulating the search formula: ('land use' OR 'agriculture expansion*' OR 'deforestation' OR 'human–environment' OR 'industrial agriculture' OR 'landscape epidemiology' OR 'urbanization') AND ('one health' OR 'public health' OR 'disease*' OR 'emerging infectious disease*' OR 'zoonoses' OR 'zoonotic disease*' OR 'H1N1' OR 'avian influenza' OR 'coronavirus' OR 'SARS') AND ('Asia' OR 'Brunei' OR 'Cambodia' OR 'China' OR 'zoonoses' OR 'Indonesia' OR 'Laos' OR 'Malaysia' OR 'Myanmar' OR 'Philippines' OR 'Singapore' OR 'Thailand' OR 'Vietnam' OR 'Southeast Asia').

socio-environmental factors, and the health of domestic animals that might cause or increase the emergence and transmission of zoonotic influenza and coronaviruses (Buse et al 2018). Through crossdisciplinary methods including field techniques, laboratory studies, and analytical approaches, One Health recognizes that barriers between human populations and other vertebrate communities are permeable, especially as human activity expands into wildland regions, destabilizing and homogenizing ecosystems (Craddock and Hinchliffe 2015). The conceptual origins of One Health in the 20th century can be traced to 19th century research by Louis Pasteur and Robert Koch, who recognized the connections between human and animal health via their work on vaccination and the etiology of infectious disease, respectively (Atlas 2012). Prior to this, studies of medicine and population health were almost always segregated by species; studies of wildlife disease focused on zoo animals and only occasionally on wild species with relevance to human diseases or livestock (Zinsstag et al 2011, Wallace et al 2015, Cunningham et al 2017).

The popularity of sustainable development to understand interdependency between humans, animals, and ecosystems further solidified One Health as the predominant health-environment framework in the 21st century. The 'One World, One Health' conference organized by the Wildlife Conservation Society in 2004 introduced the 'Manhattan Principle', a set of 12 recommendations emphasizing the significance of ecology in the prevention of epidemic and epizootic diseases (Atlas 2012, Bidaisee and MacPherson 2014, Lerner and Berg 2017). This bolstered the influence of ecology in One Health approaches by formally recognizing that health and sustainability of ecosystems and wildlife are vital to human communities and domesticated animals (Zinsstag *et al* 2011). In 2009, the American Veterinary Medical Association and the American Medical Association together established the One Health Commission, formally recognizing research programs, academic journals, and resources for disease surveillance under the One Health framework (Atlas 2012). Since then, One Health has become one of the most prominent discourses in Global and Public Health research, though with less uptake in policy and institutional circles (Bidaisee and MacPherson 2014, Galaz *et al* 2015)⁷.

One Health has also garnered many critiques (Wallace *et al* 2015). The analytical and methodological breadth of the One Health framework is a strength but can also be a weakness, as the approach remains differentially defined across disciplines⁸. While One Health is interdisciplinary in theory, it

⁷ Several other frameworks address similar challenges, including EcoHealth and Planetary Health. One of the central tenets of EcoHealth, as advanced by the EcoHealth Alliance organization, is that a planet exhausted of natural resources and with social instability is fundamentally unable to uphold human health and well-being (Charron 2012, Zinsstag 2012, Lerner and Berg 2017, Waltner-Toews 2017). Planetary Health is another approach that focuses on the health of current and future human generations alongside health equity. Unlike One Health and EcoHealth, it does not emphasize interdisciplinarity across the life and social sciences and is focused primarily on human health (Lerner and Berg 2017). ⁸ At its most narrow, one definition frames One Health at the intersection of public health and veterinary medicine, but through its evolution some conceptions have grown to include many disciplines. Coalitions such as the One Health Global Network and the One Health Commission present definitions with slight variations, with the former defining it as a method to 'Improve health and well-being through the prevention of risks and the mitigation of effects of crises that originate at the interface between humans, animals, and their various environments' (Lerner and Berg 2017, p 3) and the latter specifying collaborative efforts to optimize health for people, animals, and the environment (Bidaisee and MacPherson 2014).

emphasizes the 'human-wildlife interface' in practice, maintaining a separation between humans and non-humans in ways that reify these boundaries (Davis and Sharp 2020). It also remains difficult to implement such a broad objective, promoting human, animal, and ecosystem health simultaneously, in practice. Models attempting to analyze many elements under a single umbrella-from viruses and molecules to farms, communities, and landscapes-can quickly become unwieldy and unuseful (Scoones et al 2017, Waltner-Toews 2017). Furthermore, the framework was almost entirely conceptualized through Western research, particularly from and in the United States. There continues to be a marked gap in One Health research, application, and legitimacy in the Global South. This remains true even as, the COVID-19 pandemic notwithstanding, most of the public health and economic impacts from infectious zoonotic disease now occur in developing countries in the tropics (Bidaisee and MacPherson 2014, Davis and Sharp 2020).

In parallel to One Health, the field of landscape epidemiology has sought to incorporate nuanced analyses of land cover and landscape structure into disease research by examining the spatial dynamics of disease risk and emergence (Ostfeld et al 2005, Lambin et al 2010)9. Research in this field combines pathogen ecology at microscales and landscape ecology at macroscales to understand relationships between land cover and use and the underlying ecological processes that determine disease dynamics (Emmanuel et al 2011, Meentemeyer et al 2012, Cumming et al 2015). Land cover refers to the soil, terrain, surface, groundwater, and biotic attributes of a given land surface while land use is the human utilization of the land; landscape structure meanwhile refers to the layout and relationship between different land covers and uses, including species habitats (Lambin et al 2010, Goodin et al 2018). As McClure et al (2019) argue, land use planning for health outcomes is a neglected focus within the One Health framework despite general acceptance that land use change affects how and where disease

spreads, which landscape epidemiology has sought to address. The complexities of human behavior and decision-making, however, especially in landscapes that have been drastically changed by anthropogenic activities, complicate understanding of disease systems (Meentemeyer et al 2012) and remains a shortcoming of landscape epidemiological research. Landscape epidemiology is further limited by incomplete understanding of the relationships between zoonotic disease and human-modified landscapes (Brearley et al 2013). Because ecosystems function at multiple spatial and temporal scales, emergence and transmission of disease is shaped differently across regions and temporal scales. Analyses of land use vis-à-vis disease trajectories thus remain insufficient when they do not account for the numerous human and ecological dimensions of disease transmission, which are shaped by abiotic and biotic factors including seasonal and climatic changes that cause variation in transmission predictability across time (Parratt et al 2016). Since ecosystems have non-linear and unpredictable feedback loops for certain ecological dynamics, specific drivers of change can be difficult to measure (Meentemeyer et al 2012, Gibb et al 2020). In other words, there is no 'one size fits all' paradigm of land use and disease since the same land use changes have varying impacts on different species, which is an obstacle for landscape epidemiological modeling (Lambin *et al* 2010).

Both One Health and landscape epidemiology are poorly equipped to account for political-economic influences on land use change even though the most significant drivers are often linked to international and national governance, policy, and economic dynamics (Meyfroidt et al 2013, Zhang 2021). For instance, few studies in landscape epidemiology have included patterns of urbanization and suburbanization in analyses of land use even though changes in human settlement, labor regimes, migration, and lifestyles can alter the type and frequency of contact between human populations and animal carriers of disease, thereby increasing likelihood of zoonotic disease transmission (Murray and Daszak 2013). Lambin et al (2010) also emphasize that the relationship between land use and zoonotic disease can be influenced by land use policies, such as land tenure and different management practices on public versus private lands, yet these considerations are rarely made explicit in One Health research or landscape epidemiology. Another persistent challenge for One Health is that the disciplines best equipped to analyze such complexity at multiple scales (e.g. the qualitative social sciences) are often dismissed by biomedical and other 'hard' science or epidemiological approaches as being 'too soft', un-objective, or unable to fit into models (Waltner-Toews 2017). As Waltner-Toews (2017) argues, dominant One Health models and methods see 'One World, One Health' as a problem to be solved through more data and technological innovation; if

⁹ Contemporary understanding of infectious disease as a feature of ecological systems originates with three researchers in the first half of the 20th century. In 1933 geographer Maximilien Sorre connected geographical, biological, and sociological considerations in his discussion of 'Pathogen Complexes' (Akhtar 2003, Vanwambeke et al 2019). Building on this, Jacques May in medicine outlined 'medical geography' and the geography of disease (May 1950), followed a decade later by ecologist Evegeniĭ Pavlovskiĭ's concept of 'natural nidalities', which conceptualized disease as naturally occurring features of ecosystems that circulate among arthropods and wild species independent of human influence (Balashov 2010). Pavlovskij suggested landscapes could be useful for understanding spatial disease dynamics (Pavlovskii 1966, Goodin et al 2018). These theories on the connections between landscape and disease were extensive, but the discipline of landscape epidemiology remained largely stagnant until advances in geospatial tools revived the field in recent decades (Goodin et al 2018).

that remains the case then the emergent solutions will continue to be technological interventions that do not sufficiently address the underlying complexity embedded in socio-environmental systems, including societal inequality and environmental degradation (Wallace *et al* 2015). Underpinning this is the broader observation that much research on health, including through One Health, operates through a neoliberal, apolitical paradigm despite recognition that neoliberal political-economic dynamics themselves are drivers of landscape change, health inequity, and disease emergence (Wallace *et al* 2015, Smith 2022).

Disciplinary and paradigmatic differences in approaches to human-environment research are not easy to resolve, theoretically or in practice, particularly in addressing novel zoonotic diseases that emerge out of new socio-ecological contexts and transmit rapidly across rural and urban landscapes. There have been, however, recent calls from within the social sciences to broaden the frameworks within which scholars research viral outbreaks that respond to the critiques of One Health, directly or indirectly. Scoones et al (2017) suggest One Health could better integrate qualitative social scientific methods that highlight localized social conditions contributing to disease transmission in quantitative modeling of disease dynamics, which in turn could produce more inclusive models and thus legitimacy of models in governing zoonotic disease. Explanatory models of health outcomes and zoonotic disease emergence and transmission could further consider context and relations between individuals and factors, rather than ascribing individual agency to individuals without contextualizing their actions in broader political and economic opportunities and limitations (Senanayake and King 2019). Wallace et al (2015) propose 'Structural One Health' as a means of linking capitalist drivers of landscape alteration to changing wildlife dynamics, agriculture, and human health. While Cunningham et al (2017) call for more attention to wildlife trade and consumption in zoonotic disease research for instance, this would only be productive if it moved beyond xenophobic cultural assumptions that have often underpinned Western research on wildlife-as-food (see also MacGregor and Waldman 2017, Wu 2021). Finally, recent work in health geography shows that pandemics need to be re-thought with more attention to urban space, processes of global urbanization, and international institutions given that cross-scalar governance and climate change are interrelated factors that strongly impact viral transmission by exacerbating inequality and affecting community health and sanitation resources (Connolly et al 2021, Wu 2021, Ruszczyk *et al* 2022).

An additional way forward is through political ecology approaches, which have rarely been in direct conversation with research adopting a One Health framework. Political ecology is a sub-field at the intersection of geography and anthropology that attends to how environmental change is produced through differential, uneven access to and control over natural resources, which in turn is shaped by political and economic dynamics operating across scales. In applying this to studies of human health and disease, King (2010) argues that political ecology offers 'a needed framework for understanding how social and environmental systems intersect to shape health across spatial and temporal scales' (40), generating new ways of understanding how discourses about health are produced by powerful actors and institutions. While research in political ecology of health has proliferated in recent years (Kaup 2018, 2021, Ferring and Hausermann 2019, Nichols and Casino 2021), relatively few studies in the field have taken viral pandemics, and coronaviruses and influenzas in particular, as their objects of analyses. Through multi-scalar analysis and mixed methods including ethnography, biophysical approaches, Geographic Information Systems, and spatial data analysis, a political ecological framework can reveal, however, how social, political, cultural, and environmental dynamics contribute to the spread of disease across a landscape. This includes migration patterns and violence that disrupts livelihoods and health care provisioning, as well as larger-scale dynamics such as state and economic agendas that enable class and racial divisions, which in turn leads to disease transmission and differential health outcomes (Davis and Sharp 2020). Political ecology of health frameworks also attend to differences in discursive understanding of disease between global, national, and local interests, the latter of which can challenge normative or orthodox understandings of disease produced by powerful institutions that in turn shape public health interventions (King 2010, Leach et al 2010, Leach and Scoones 2013, Jackson and Neely 2014, Leach 2015, Neely and Nading 2017). Connolly et al (2021) further propose landscape political ecology as a framework for studying infectious disease that attends to the extended temporal and spatial processes of urbanization and how they affect broader socio-ecological systems, particularly in the Global South, which in turn enables the spread of infectious disease (see also Gandy 2022). Zhang (2021, p 6) goes further, arguing that understanding pandemics 'requires a critique that delves deeper than global capitalism alone and into the heart of discourses about modernization, development, environmental degradation, and the prospects for global health and sustainability in the new century'. As the Covid-19 pandemic is likely to continue to draw attention to research on current and future zoonotic disease, we encourage scholars taking up this research to consider these frameworks that extend beyond the dominant One Health perspective as a means to better understanding the cross-scalar, political-economic, and complex human–environment interactions that impact the human-wildlife interface and thus contribute to the emergence of viral zoonoses and possible pandemics.

4. Biodiversity and emergence of viral zoonotic disease

Globally, there are likely hundreds of undiscovered viruses with the potential to infect humans, with the highest zoonotic potential found in viruses harbored by domesticated species, primates, bats, mustelids, racoons, rodents, armadillos, and pangolins (Johnson et al 2020, Munnink et al 2021)¹⁰. All zoonotic pathogens must overcome a hierarchical series of barriers to cause spillover infections in humans. Volpato et al (2020) argue that at least two conditions need to be met for this to occur: one, generalized human exposure to wildlife due to human activities, such as logging, mining, and agricultural expansion, into forested areas and two, direct exposure to wildlife through, for example, consumption of wildlife meat or through exposure to wildlife excrement in forested areas or caves. Plowright et al (2017) classified two major groups of infectious disease from freeliving wildlife based on epizootiology criteria: one, zoonotic spill-over (via excretion and slaughter) from wildlife populations to domesticated animals living in close proximity; and two, EIDs related directly to the encroachment of human activities, such as into forested areas via host translocations. Understanding how the species barrier is functionally and quantitatively crossed, and how different species interact in space and time, could improve the ability to predict or prevent future spillover events (Plowright et al 2017).

The concentration of undiscovered zoonotic viruses is presumed to be highest in regions with high biodiversity, or species richness, which correlates with tropical areas, reflecting assumptions that pathogen diversity correlates with host diversity (Murray and Daszak 2013, Hosseini et al 2017). SEA is significant regarding global biodiversity, with four of the world's 25 biodiversity hotspots located in the region and a projected 40% species loss by 2100 (Jones et al 2008, Coker et al 2011, Estoque et al 2019, McElwee et al 2020). While causal relationships between specific land use changes and zoonoses emergence remain ill-defined in relation to host diversity and species composition, there are reasons to believe that land use plays a significant role in the emergence and transmission of zoonotic disease (Gibb et al 2020). First, zoonotic viruses can be assessed at both macro and micro scales within landscapes. At the macro

scale, ecosystem condition and human activity within ecosystems can reveal why a disease emerges where it does, while research at the micro scale, focusing on specific pathogens, can show how pathogens are connected to biodiversity or species composition (Machalaba and Karesh 2017). The source of zoonotic viruses can be either a reservoir, which refers to the original source of the pathogen (typically an organism that is not negatively affected by the pathogen) or an 'incidental host', which is a carrier of the pathogen. Though they may be susceptible, incidental hosts do not typically become very ill. From an ecological standpoint there is nothing inherently threatening about pathogens: relationships between pathogens and hosts are naturally occurring and pathogen infection of new hosts is a critical component of their survival. Human activities within ecosystems changes the dynamics of spillover, however (Machalaba and Karesh 2017).

Changes in landscape structure can alter biodiversity and thus affect the force of infection (FOI), or the ease of transmission, between zoonotic pathogens and human populations (McMahon et al 2018). A comprehensive understanding of the FOI involves a consideration of 'pathogenicity', which describes how characteristics of infectious disease are shaped by many factors extrinsic to the pathogen itself (Lambin *et al* 2010, Davis and Sharp 2020). Lambin *et al* (2010) outline both a static and a dynamic view of pathogenicity: the former describes an overlay of static spatial distributions of vectors and their habitats, animal hosts and their habitats, and vulnerable human populations and their land use, while the latter focuses on temporal and spatial relationships at multiple scales. When pathogenicity is applied in this way, the landscape becomes a proxy between disease reservoirs, vectors, and hosts.

Features about biodiversity are defined by landscape structure, which in turn is shaped by cultural and economic dynamics that prompt land use change. Landscape heterogeneity is thus key to determining biodiversity. As a characteristic of landscape structure, it describes the degree to which the landscape is composed of a combination and mixture of disparate elements, habitats, or land cover classes (Syrbe et al 2013). Species respond differently to changes in landscape structure, with some responding more to the makeup of their habitat and others responding to arrangement, size, and shape of different landscape attributes (Syrbe et al 2013). A diversity of landscape attributes can also influence the dynamics of transmission of infectious diseases by either confining or spreading disease (Lambin et al 2010). The composition and configuration of ecosystems in the landscape influence species level and genetic biodiversity. Parratt et al (2016) point out that landscape heterogeneity is an important factor in disease risk, including epidemiological interactions and evolutionary paths of disease. This is particularly true in ecotones,

¹⁰ Morand *et al* (2014) found that richness of infectious disease was positively correlated with bird and mammal diversity, while outbreak of disease was correlated with the number of *threatened* bird and mammal species specifically.

or regions of transition between ecosystems. When combined with fragmented landscapes (small, disconnected parcels of land cover) these spatial conditions create 'hotspots' for pathogen spillover (Parratt et al 2016, Borremans et al 2019). The spatial configuration of the landscape parcels, not just their size, are therefore crucial for understanding disease dynamics. Habitat connectivity for vectors and hosts also shape disease risk (Lambin et al 2010, Borremans et al 2019). Meentemeyer et al (2012) distinguish between structural connectivity, or the physical attributes of landscapes that do not explicitly reveal how organisms move among those landscape features, and functional connectivity, which examines how landscape features so facilitate or hinder the spread of pathogens. Land use change, particularly deforestation, creates larger ecotones and more fragmented patches, allowing for pathogen spillover by increasing encounters between wild and domestic animals (Patz et al 2004, Borremans et al 2019, Santiago-Alarcon and MacGregor-Fors 2020).

There are two schools of thought regarding the explicit role of biodiversity in zoonotic disease emergence: dilution and amplification. The former refers to a decrease in disease prevalence as a function of higher biodiversity, while the latter refers to an increase. In conditions of ecosystem disturbance, either dilution or amplification can occur. Dilution frames disease regulation as an ecosystem service, suggesting that the variety and abundance of host species 'buffers' the spread of pathogens through a high ratio of competent to non-competent species (Cunningham et al 2017). Ecosystem communities with large numbers of non-competent host species potentially reduce disease transmission by increasing the rate of transmission to non-competent species, which lowers the infection rate in competent hosts and subsequently lowers the risk of zoonotic 'jumping' to humans (McMahon et al 2018). Most published research to date supports the dilution hypothesis. According to Pongsiri et al (2009) 'biotic homogenization' is a threat to the efficacy of the dilution effect. This occurs when exotic or invasive species threaten local communities, which reduces biodiversity at both the genetic and species levels. Reduced predation and competition can increase abundance of competent hosts, reducing the buffering effect on disease transmission and thus emergence in human populations (Horby et al 2013). Lower genetic diversity can also make individual animals more susceptible to existing or novel diseases (Brearley et al 2013). Amplification, meanwhile, is the opposite of dilution, hypothesizing a positive correlation between biodiversity and infectious disease risk (Rohr et al 2020). Amplification thus hypothesizes that the threat of transmission increases with higher biodiversity because there are more viable hosts, which allows a pathogen

to develop optimal virulence¹¹. This also suggests that some host species benefit from declines in biodiversity through reductions in predatory species or other changes in landscape structure. In both the dilution and amplification theories, the relationship between biodiversity and disease transmission is often non-linear and highly dependent on particular ecosystem contexts, surrounding land uses, and the disease in question (Rohr *et al* 2020).

Two other hypotheses about the relationship between human interference in ecosystems and emergence of zoonotic viruses are the pathogen pool (or pathogen pollution hypothesis) and the perturbation hypothesis. The former describes the anthropogenic movement of pathogens to new locations since the introduction of novel pathogens to biodiverse regions can impact diversity of disease (Brearley et al 2013, Cunningham et al 2017, McMahon et al 2018). In some cases, the introduction of additional host species can reduce transmissions of local diseases, but novel species also present a significant risk of introducing novel pathogens (Pongsiri et al 2009). The perturbation hypothesis, meanwhile, refers to the indirect impact of land use change on biodiversity. It proposes that land use changes alter disease dynamics by changing multi-host disease transmission modes and rates of spread (McMahon et al 2018). It also focuses on contact rates and novel exposures rather than disturbances to pre-existing community composition (Murray and Daszak 2013). While both hypotheses are accepted as valid, the degree to which each impact zoonotic disease emergence remains understudied. Although the pathogen pool hypothesis and the perturbation hypotheses pertain to different processes (species introduction and land use change, respectively), land use activities that reduce biodiversity may increase humanwildlife interaction and introduce new host species, leading the two hypotheses to potentially work in tandem (Hosseini et al 2017). Furthermore, through both pathogen pool and perturbation, natural selection constantly alters pathogen-host dynamics and creates novel 'fittest' strains adapted for new environmental conditions and host species (Patz et al 2004).

There are several interrelated causes of changes in landscape structure and associated biodiversity loss in SEA and China. Habitat destruction and human encroachment into forested ecosystems may introduce new diseases to wildlife populations, generating

¹¹ While dilution is the dominant hypothesis overall, Faust *et al* (2017) indicate the possibility of a publishing bias towards articles that support the dilution hypothesis. Regardless, the theory of dilution is not considered to be universally applicable, and its validity is likely pathogen dependent (Brearley *et al* 2013, Faust *et al* 2017, Hassell *et al* 2017, Gibb *et al* 2020, Santiago-Alarcon and MacGregor-Fors 2020).

disease reservoirs that also cause disease transmission to domesticated animals (Rohr et al 2019). Destruction and fragmentation of habitat can also change gene flow and contact between species while reducing overall biodiversity. The intentional or accidental introduction of invasive species, such as rats and pigs, into wildland areas, by humans alters community ecology and diversity, and in some cases these groups act as a bridge for zoonotic disease transmission between wildlife and human communities (Hosseini et al 2017). Beyond habitat destruction and non-native species invasion, wildlife poaching may be a significant source of biodiversity loss among animal species with cascading impacts on ecosystems, though the specific dynamics of how and how much remains understudied (McEvoy et al 2019). SEA and China have the world's highest rate of wildlife declines, with more than one million animals, especially mammalian species, exported both legally and illegally from 2014 to 2018 (Nijman 2010, Symes et al 2018, CITES 2021). Vietnam, Indonesia, Malaysia, and China are the largest exporters of wild-caught animals, while Japan and the European Union are the largest importers; however, as we discuss in a later section, much of the wildlife caught in China and SEA is traded and consumed domestically or within the region as food, fashion products, traditional medicine, and pets (Vu and Nielsen 2018, CITES 2021, Jiao *et al* 2021).

As Vanwambeke *et al* (2019) argue, a more complete understanding of zoonotic disease emergence should be examined in a broader context of land use change. In summary, recent research from landscape epidemiology indicates that higher rates of biodiversity generally reduces the risk of zoonotic virus transmission to humans in part through the dilution effect: the more species there are, the less likely one virus will emerge as dominant. As we discuss in the next section, peri-urbanization and industrial agriculture contribute to biodiversity loss at both species and genetic levels throughout SEA and southern China, thus exacerbating the risk of zoonotic virus emergence and transmission to humans.

5. Land use change as a driver of viral zoonotic emergence

The connections between land use change and zoonotic disease emergence in Asia are complex, ongoing, and not always linear or predictable. While ecological conditions underlie emergence of all zoonotic disease, political-economic factors, including global trade and market expansion, public trust in governance or lack thereof, and infrastructure development drive land use changes, which influence ecological conditions, including biodiversity, and thus zoonotic disease outbreaks (Hassell *et al* 2017, Connolly *et al* 2021). About 15% of the world's

tropical forests-hotspots of biodiversity-are found in SEA, with extensive losses over the past several decades of lowland forests, highland forests, forest fragments, and protected areas (Potapov et al 2017, Zeng et al 2018, Estoque et al 2019, Hansen et al 2020, Namkhan et al 2021). As deforestation has increased, so have incidences of zoonotic disease transfer to humans: an estimated 50% of all recorded zoonotic diseases have emerged since 1940, which correlates with vast tropical forest loss (Jones et al 2008). Drivers of deforestation and associated land use change in SEA and southern China include industrial agricultural expansion, timber extraction, mineral and fossil fuel extraction, dam and road construction, demand for fuelwood, urbanization, and conversion of diversely cropped smallholder agricultural lands to monoculture plantations (Patz et al 2004, Kenney-Lazar and Ishikawa 2019, Davis et al 2020). The vast conversion of forest to commercial agricultural land in developing countries, especially in SEA, is most often driven by the production of agricultural commodities like oil palm and pulpwood (Meyfroidt et al 2013, Vijay et al 2016, Meijaard *et al* $(2020)^{12}$.

In SEA and southern China, broad politicaleconomic dynamics enable these changes in land cover, land use, and thus human-wildlife interaction, which in turn influences opportunities for zoonotic disease emergence (Morand and Lajaunie 2021). Deforestation, for instance, whether resulting from agricultural expansion, logging, or urban development, results in the loss or abandonment of animal roosting sites and the loss of feeding habitats. Land cover also influences the population dynamics of reservoir species, especially of wild mammals, increasing or decreasing the risk of interspecies encounters and zoonotic spillover (Goodin et al 2018). As with other ecosystem services, biodiversity is influenced by the structure and geographical context of the landscape including, for instance, the arrangement of land use 'units' within the landscape (e.g. fruit orchards, monocrop fields, and wildlife habitat buffer zones) (Syrbe and Walz 2012). Below, we identify two primary drivers of shifts in land use in SEA and southern China that emerge in the literature as influential for zoonotic disease emergence: urbanization and agricultural expansion and intensification.

¹² The role of oil palm in land use change across Southeast Asia and the region's role in the production of this global commodity is vast: Indonesia and Malaysia together produce more than 90% of the world's palm oil and approximately 70% of land used for oil palm is in SEA (Vijay *et al* 2016, Meijaard *et al* 2020). States and state-sanctioned business—along with agribusinesses, biofuel enterprises, and private developers—have purchased or leased land throughout Southeast Asia, facilitating agricultural land concentration for global market production, with negative impacts on small farmers and the environment (Wallace *et al* 2015, Kenney-Lazar and Ishikawa 2019).

5.1. Urbanization

Between 1965 and 2016, the urban population in Asia grew from 430 million to 2.1 billion, a fivefold increase, with half of the region's population living in urban areas as of 2015 (Sumeet et al 2017). Predictions for 2050 project a 65% increase in the urban share of the world's population, with 90% of this growth concentrated in Africa and Asia (Ahmed et al 2019). Urbanization can be both a cause of health vulnerabilities and a means of improving health. The potential benefits of urbanization are dependent on many factors, including hygiene and sanitation, social safety nets, food security, and land ownership (Santiago-Alarcon and MacGregor-Fors 2020). The 'urban advantage' theory purports that urban areas have better health conditions than rural areas due to economic growth, but the term can also mask intra-city health disparities (Ahmed et al 2019). Connolly et al (2021) argue, however, that urbanization contributes to infectious disease spread along three primary dimensions: demographic change, infrastructure (particularly transport infrastructure that connects disparate regions, including airports and rail lines), and governance and political economy. Urbanization in lower-income countries, such as most of those in SEA, is especially challenging from a health perspective, as urban growth typically outpaces economic growth, which leads to resource constraints, insufficient planning, and inadequate sanitation infrastructure (Alirol et al 2011).

In general, understanding of the relationship between urbanization and zoonotic disease emergence in urban areas is limited by several issues (Ahmed et al 2019). One, there is a lack of consensus on what constitutes 'urban' areas. Peri-urban, places in transition from rural to urban land use types, and suburban areas are not easily designated because they are made up of large city sprawls, smaller towns and villages, and related human settlements (Alirol et al 2011, Mackenstedt et al 2015, Santiago-Alarcon and MacGregor-Fors 2020). Connolly et al (2021) point out that central urban areas have less biodiversity than peri-urban and suburban areas: compared with those in central urban areas, communities living in peri-urban and suburban areas are more likely to encounter wildlife and thus have a higher likelihood of zoonotic exposure. Central urban areas are also likely to have better established public health and medical infrastructure that can contain early outbreaks and transmission (Connolly et al 2021, Ruszczyk et al 2022), though this was not the case in the initial outbreak of COVID-19 in Wuhan, China, a city of 11 million inhabitants. Yet in other ways, urban areas may have poorer poultry management than rural areas and depending on the strength of local governance structures, poor disease management capability (Finucane et al 2014). Spencer *et al* (2020) found that there was a strong quantitative correlation between areas in Vietnam that were in the midst of transitioning from agrarian to urban infrastructure and outbreaks of poultryrelated highly pathogenic avian influenza (HPAI), such as H5N1. While they measured many factors illustrative of the urban transition in rural villages, including household sanitation and water infrastructure, prevalence and modernization of poultry raising, education, and housing construction materials, with sanitation measures coupled with overall accumulation of household wealth correlated with the largest reduction in HPAI risk. Spencer et al (2020) demonstrate that the long process of urbanization can be chaotic, with lack of clear governance measures and incomplete household and neighborhood infrastructure; places in urban transition, more than traditional agrarian villages or fully urbanized cities, may thus be at highest risk for zoonotic disease exposure.

Significantly for potential zoonotic disease spillover events, peri-urbanization and suburbanization are often accompanied by deforestation and habitat fragmentation, with losses of biodiversity correlating with an increase in human populations (Mackenstedt et al 2015). Thus, urbanization typically results in two major ecological changes: the appearance of new niches through perturbation and the adaptation of pathogens to niches which are new to them, also known as changes in the pathogen pool (Vanwambeke et al 2019). Rapid expansion of urban centers can move populations in close proximity to the zoonotic systems in adjacent rural areas (Alirol et al 2011). Cities or urban centers that are surrounded by agriculture or wildland have been found to have higher chances of zoonotic disease emergence, especially in regions like SEA where there are high levels of biodiversity (Wu et al 2017, Santiago-Alarcon and MacGregor-Fors 2020). Peri-urban areas pose a specific risk of emerging infectious diseases like SARS, avian influenza, and swine flu since wildlife can well adapt to peri-urban areas and peri-urban land uses can bring humans into direct interaction with wildlife (Sumeet et al 2017, Vanwambeke et al 2019). Though most animal species are negatively impacted by urbanization, generalist species, 'urban adapters', and 'urban exploiters' are highly adaptable and attracted to peri-urban areas, with their abundant supplies of food and shelter (Mackenstedt et al 2015).

Additionally, rural to urban migration, driven in part by growth of urban centers, can exacerbate disease spread by introducing pathogens of a rural origin to a dense human population (Ahmed *et al* 2019). Circular migration between urban and rural areas in the region can facilitate the transfer of disease from wildland or rural areas to urban settings, which can facilitate rapid disease transmission among populations of migrant workers and the possibility of amplified virulence (Horby *et al* 2013). Rapid urbanization and related migration patterns thus have the potential to introduce entire populations to unfamiliar environments, which can lower local immunity while increasing human connectivity and density, and thus the potential for a zoonotic spillover event to lead to a pandemic (Cascio *et al* 2011, Wu *et al* 2017).

The relationship between growing urbanization in Asia and zoonotic disease emergence is thus not limited to expanding urban land use footprints into wildland areas and associated biodiversity loss: urbanization also transforms people's relationship to wildland areas through changes in livelihood opportunities, migration patterns, and production and consumption within food systems (Mishra et al 2021). For instance, as mentioned previously, wildlife poaching and trade impacts ecosystem biodiversity throughout SEA. Increasing economic affluence in China, Vietnam, and Indonesia has led to rising wildlife consumption for food and medicine among urban consumers (Drury 2011, Shairp et al 2016). Field (2009) found that rural to urban demographic shifts, along with rising disposable incomes, has led to increased consumption of wildlife in China's largest cities. As people moving from southern China to Beijing for greater economic opportunity bring their desire for ye wei-'wild taste' associated with prosperity and health benefits-with them, this leads restaurants and the supporting wildlife trade to increase supply and access to these foods (Zhu and Zhu 2020). This phenomenon has also occurred alongside the Chinese diaspora to cities throughout SEA as well (Vu and Nielsen 2018, Gorton et al 2011). Relatedly but conversely, however, Anagnostou et al (2021) argue that political exclusion, global conditions of structural poverty, and rising inequality in local and regional contexts, including through increased unemployment as a result of the COVID-19 pandemic, can lead marginalized communities to pursue wildlife crime, such as poaching, as a livelihood strategy. While consumption of wildlife in Asia is a millenniaold practice, it assumes new risks as a source of zoonotic disease amid extensive landscape change, human migration, and the speed at which animals and humans-and thus pathogens-can travel (Zhu and Zhu 2020).

5.2. Agricultural expansion and intensification

Increasing urbanization has consequences for land use change elsewhere, particularly in relationship to changing agricultural production and food systems, which in themselves enable the emergence and spread of zoonotic disease. Links between agricultural expansion and urbanization are a feedback loop: expanded agricultural production, often through land and forest clearing, enables urban growth and urban growth demands agricultural expansion, including for livestock (Silbergeld 2019). In rapidly urbanizing China, for example, annual per capita meat consumption is now well over the world average whereas four decades ago, most of the population ate meat once or twice per year (Schneider 2017, Rulli et al 2021). Agriculture—including subsistence, market-based, and wage-labor-is a vital livelihood for many in low- and middle-income countries, with up to one third of their populations involved in agricultural activities (Grace 2019). While agriculture and food systems have generally been an under-studied topic in infectious disease research (Bidaisee and MacPherson 2014), agricultural intensification and expansion is a significant driver of land use change and of changing interactions between humans, wildlife, and domesticated animals globally (Morand and Lajaunie 2021).

The specific biological mechanisms of how zoonotic pathogens spread from wildlife to domesticated livestock and then to humans has not always been well documented (Pulliam et al 2012). Shah et al (2019) found that people in SEA working or living in agricultural landscapes are 1.74 times more likely to be infected by a zoonotic pathogen, with these risks being greatest for those working in rubber, palm oil, and non-poultry livestock agriculture. Morand and Lajaunie (2021) found that in Asia, monoculture plantation land, including for oil palm and reforested areas planted with single tree species, show a clear connection to zoonotic outbreaks in Indonesia and Malaysia but not in Vietnam, Thailand, and southern China, likely due to biodiversity loss. In a model of horseshoe bat habitat, a known carrier of SARS-CoVs, and forest fragmentation due to livestock expansion and urban growth, southern China and Indonesia (Java and southern Sumatra) have the highest risk of human-wildlife spillover events due to the co-occurrence (but not necessarily causal) of livestock density, human settlements, and forest fragmentation (Rulli et al 2021). Risk of zoonotic exposure for agricultural laborers is also linked to poverty through 'biodiversity-poverty-disease feedbacks', which describes relationships between socioeconomic status, biodiversity loss, changes in soil quality, and infectious disease (Rohr et al 2019). Rural and poor people also rely more heavily on directly obtaining natural resources for livelihoods, leading to closer contact with wildlife (Yang et al 2015).

The most significant agricultural transition in SEA and China is the 'livestock revolution', or the development of industrialization of animal breeding and mass distribution of animal food products (Wallace *et al* 2015). Between 1961 and 2017, global annual meat consumption grew seven-fold, from 70 billion kg to almost 500 billion kg (Zhang *et al* 2020). In most instances, agricultural transition is a feedback loop, beginning with income growth in developing countries, which is associated with higher meat consumption (Silbergeld 2019). Nearly 50% of

animal products globally are produced in Asia, with a heavy concentration in China (Aiyar and Pingali 2020)¹³. Livestock farming is common in most Southeast Asian nations (except Singapore and Brunei) with 50% of households in the region involved with livestock, particularly chickens; 60% of overall livestock production is maintained by smallholder farms, which makes monitoring and preventing disease outbreaks difficult (Hassan 2014). In general, this dietary transformation has been facilitated by shifting away from free-range animal rearing near urban centers towards capital-intensive, monoculture, and highvield models that favor vertical integration with an emphasis on contract farming where workers and livestock are confined to production facilities together (Silbergeld 2019). Through high animal concentrations, mechanical innovations, and the use of specialized animal feeds and additives, large-scale highintensity animal farming has achieved much higher outputs than small-scale farming, bringing down meat prices. In Asia this is particularly true for poultry and pigs (Petrikova et al 2020).

Domesticated animals play a potentially significant role in bridging the epidemiological gap between wildlife and humans (Morand et al 2014). Livestock breeding at larger scales can lead to deforestation and encroachment into wildlife habitats, increasing contact rates between humans, domesticated animals, and wildlife that may carry infectious disease (Cascio et al 2011). Domesticated livestock and pets can also act as amplifying hosts by facilitating the evolution and adaptation of emerging diseases originating in wildlife (Hassell et al 2017). Morand et al (2014) found a positive correlation between the time since mammal domestication and the total number of parasites or infectious diseases they shared with humans. The density of industrialized animal confinement favors rapid transmission of zoonotic disease while poor governance of food safety regulations has increased the emergence and spillover of infectious disease (Silbergeld 2019, Aiyar and Pingali 2020). For instance, industrial agriculture generates large amounts of animal waste and biosolids, which have been linked to some emergent diseases, including influenza (Li 2017). 'Productivity enhancements', such as selective breeding to increase livestock yields, reduce genetic diversity, with implications for zoonoses (Aiyar and Pingali 2020). In the poultry industry, selective breeding has generated masses of genetically similar animals living in close proximity, which is an ideal condition for the evolution of relatively harmless viral and bacterial pathogens into virulent strains (Li 2017, Vanwambeke et al 2019). Industrial agriculture also relies on antibiotic use and

extensive meat processing, both of which can act as a reservoir for viral and antibiotic-resistant bacterial pathogens (Founou et al 2016). Management of livestock also may affect the probability of exposure and disease. Interventions to decrease the probability of virus spillover can be implemented at multiple levels from targeting the reservoir host to managing recipient host exposure and susceptibility (Plowright et al 2015). Even if there is no spillover of emerging infections from infected livestock, there is a potential for losses due to disease, from either natural death or preventative culling. This can threaten food supplies and income, especially for smallholder and subsistence farmers, with implications for regional migration and increased contact with wildlife (Rohr et al 2019, Aiyar and Pingali 2020).

One zoonotic disease outbreak associated with domesticated animals is the NiV virus, a paramyxovirus which negatively impacts neurological and respiratory functions in humans that first emerged in Malaysia in 1998. It caused significant outbreaks in both humans and domestic pigs, and massive economic loss for the pig industry as over one million pigs were culled in Malaysia (Chua et al 2002). It is widely accepted that the primary wildlife reservoir for NiV is pteropid fruit bats, also known as flying foxes. Land use changes in the region have changed the behavior and distribution of pteropid species: prior to the 1998 outbreak, their habitat in SEA had been in decline due to land clearing for pulpwood and oil palm plantations. This, combined with dry climatic conditions associated with that year's El Nino Southern Oscillation, is believed to be one of the primary drivers of the outbreak. More specifically, Chua et al (2002) found that many of the piggeries linked to the outbreak demonstrated clear interactions between wild animals and livestock, as they were situated in durian farms and rambutan orchards. Fruit partially eaten and discarded by bats were found in pig enclosures, suggesting a possible mode of transmission. This speaks to the risks of agricultural expansion in which land is dually used for commercial (as opposed to subsistence) livestock and fruit production (Pulliam et al 2012). In the case of NiV, overlapping land use for piggeries and fruit orchards was widespread in Malaysia; between 1970 and the late 1990s, the production of pigs and mangoes both tripled. Furthermore, declining production of both pigs and mangoes between 1998 and 1999 suggests a reduction in mango production following culling and abandonment of piggeries following the outbreak. Currently, NiV is one of the only WHO priority diseases that has remained largely endemic to SEA but retains pandemic potential due to host and geographic adaptability and high potential for human-to-human transmission (Pulliam et al 2012).

Another example of overlapping livestock and other food production systems, the emergence of H5N1 avian influenza in southern China in the 1990s

¹³ Global demand for dairy and meat products is expected to double from 2020 to 2050, due to changing eating habits by urban residents in developing countries in Asia and Latin America (Grace 2019).

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has been traced to domesticated geese production, which often occurs in or near rice paddies in China and SEA (Gilbert *et al* 2008). The rapid intensification of animal food production systems and urbanization, combined with climate vulnerability, in SEA and southern China will undoubtedly change the landscape of zoonotic disease, introducing both new opportunities for control and prevention as well as new vulnerabilities for disease emergence and spread (Carrique-Mas and Bryant 2013).

6. Discussion

In this review we synthesized recent scholarly research on how large-scale changes in land use may lead to increased likelihood of viral zoonotic emergence in SEA and southern China. This paper shows that biodiversity is one key factor in shaping whether a zoonotic pathogen becomes virulent enough to cause spillover event from wildlife to humans. Furthermore, urbanization and agricultural expansion and intensification are two broad types of land use change that impact biodiversity as well as influence the proximity between humans and wildlife. Evidence suggests that most zoonotic pathogens that have caused infectious respiratory disease in humans and became regionally or globally prevalent-primarily influenza and coronaviruses-initially jumped from wildlife to humans in southern China or SEA. These spillover events, and the opportunity for them to spread rapidly among a globalized population, have become more frequent in recent decades as large-scale land use changes bring humans into more frequent and closer contact with wildlife hosts.

While we delineated existing research that influences the human-wildlife interface into three broad categorical phenomena-biodiversity, urbanization, and agricultural expansion and intensificationthese phenomena are highly interrelated, iterative, and self-reinforcing, making it difficult to isolate them as causal variables of zoonotic disease emergence in practice. Not all zoonotic pathogens become diseases in humans, and not all diseases become pandemics: as Zhang (2021, p 33) writes, social complexity is 'required to transform a "pathogen" into a disease'. Literature discussed in this paper shows that in fact, the social-economic and ecological dynamics in interaction are required to transform a pathogen into a disease, and a disease into a pandemic. For instance, as agricultural production shifts from smallholder-based to large-scale commercial plantations and livestock holdings, that shift reduces overall biodiversity in the region, increasing likelihood that a single zoonotic pathogen can spillover into human populations. But the shift to industrial agriculture may also drive other changes that influence the human-wildlife interface. For example, this agrarian change might lead women who were once participants in smallholder agricultural labor regimes to

migrate to urban centers for higher paying domestic work, while men (and sometimes families) seek new sources of income, such as from mining, that increasingly exploit remote forested areas and subsequently alter ecosystem structure. In such an instance, human exposure to zoonoses-carrying wildlife becomes more probable because one, activities that cause forest fragmentation, like mining, can reduce biodiversity and two, lower biodiversity leads to higher pathogen incidence and virulence via the dilution hypothesis. Changes in land use, in other words, should not be considered in isolation from one another or as simply changes to landscape structure within that area. Changes in land use have significant cascading impact on people's livelihoods and migration patterns, which in turn has consequences for biodiversity and ecosystems in both proximate and distant places as well as impacts on the type and frequency of human-wildlife encounters.

Considering that in the coming years there will likely be forthcoming research on zoonotic viruses, both related to uncovering the origin story of COVID-19 and on preventing and predicting the next pandemic, this paper makes a substantial contribution towards these new research agendas. One Health, a framework conceptualizing human health as a function or outcome of ecosystem health, has become a predominant approach in healthenvironment research, alongside landscape epidemiology. Yet our review revealed critical knowledge gaps in zoonotic disease emergence that One Health might not be well positioned to respond to without drawing in additional conceptual approaches that better consider the structural, cross-scalar, and politicaleconomic drivers of land use change and the shifting human-wildlife interface. We thus suggest that there is much room for future research that integrates qualitative, multi-scalar questions and data collection with quantitative research in models of land use change and localized investigations of host-pathogen relationships and their potential for viral zoonotic spillover events.

7. Conclusion

Through a review of literature on land use, including urbanization and agricultural expansion, and zoonotic disease emergence in SEA and southern China, this article argues that three structural and interrelated land use changes enable an increased likelihood of viral zoonotic spillover events at the human-wildlife interface: biodiversity loss, urbanization, and agricultural expansion and intensification. This region has been a hotspot of zoonotic pathogen emergence over the past century, with most of the regional and global pandemics of influenzas and coronaviruses originating here. Understanding that past and future zoonotic spillover events at the human-wildlife interface, and their

potential for rapid human-to-human transmission, are a function of interrelated ecological, social, and political-economic processes is critically important for preventing the next pandemic. Processes of urbanization and commercial agricultural expansion have clear impacts on the human-wildlife interface through changes in ecosystem structure, forest fragmentation, and increased proximity of humans, livestock, and wildlife. Yet these land use changes should not simply be understood as expanding footprints of human activity into previously forested or wildland areas. Given the far-reaching implications for global human health, a robust future research agenda on zoonotic disease emergence should thus go beyond predominant One Health frameworks that consider human health and environmental change together, to include global and regional-scale political economic drivers of land use change, and their consequences for human-wildlife interaction in rapidly changing ecosystems at local scales.

Data availability statement

No new data were created or analyzed in this study.

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