Land use change and livestock revolution as contributors to Coronavirus emergence risk

Maria Cristina Rulli (✉ cristina.rulli@polimi.it)

Politecnico di Milano

Paolo D'Odorico

University of California, Berkeley <https://orcid.org/0000-0002-0007-5833>

Nikolas Galli

Politecnico di Milano <https://orcid.org/0000-0002-6746-5350>

David Hayman

Massey University

Article

Keywords: COVID19, Livestock, Land Use Change, One Health, Wildlife

Posted Date: September 18th, 2020

DOI: <https://doi.org/10.21203/rs.3.rs-69560/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Version of Record: A version of this preprint was published at Nature Food on May 31st, 2021. See the published version at <https://doi.org/10.1038/s43016-021-00285-x>.

Abstract

The recorded number of epidemics from emerging diseases is increasing at alarming rates, posing new threats on human societies. Despite the consensus on the existence of a nexus between emerging diseases and human pressure on the environment, the link to global and regional trends in food demand and agricultural production remains poorly understood. The ongoing severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) pandemic (COVID-19) is no difference. SARS-related coronaviruses are mostly discovered in Asian horseshoe bat species. It is unclear to what extent the transmission to humans is facilitated by ongoing land use and animal husbandry trends underlying recent shifts in the food system. Forest fragmentation, human encroachment into wildlife habitats as a result of expanding urbanization, cropland, and concentrated animal farming are hypothesized to favor the emergence of zoonotic diseases. In the regions of the world populated by Asian horseshoe bats (>28.5 million km^2), we analyze comprehensive high-resolution (30m-1000m) datasets on forest cover, cropland distribution, livestock density, human population, human settlements, bat species' distribution, and land-use changes to explain why China was and remains at risk for SARS-coronavirus outbreaks. We show that in China areas populated by horseshoe bats exhibit statistically significant higher forest fragmentation and concentrations of livestock (e.g. poultry and pigs) and humans than other countries. Moreover, regions of China populated by horseshoe bats are hotspots of forest fragmentation, livestock density, and human settlements. These results are consistent with the notion that population growth and increasing meat consumption associated with urbanization and economic growth have expanded the footprint of agriculture, leading to human encroachment in wildlife habitat and increased livestock density in areas adjacent to fragmented forest patches. These results indicate that conditions in China put it at high risk for SARS-related coronavirus transmission to humans because land use patterns reduce the distance between wildlife reservoir species and humans.

Background

The ongoing severe acute respiratory syndrome coronavirus-2 (SARS-CoV-2) pandemic is claiming human lives and disrupting the functioning of human societies in unprecedented ways. Where did this virus come from and how did it transmit to humans? What facilitated such a host shift and how can we prevent this from happening again? To what extent can the virus transmission from wildlife to humans be facilitated by ongoing land use and animal husbandry trends underlying recent shifts in food systems? These are important questions, in addition to the most outstanding ones about whether, when, and how this pandemic will end.

Recent years have seen a rise in the recorded number of epidemics from emerging diseases. Such epidemics constitute a major public health threat because of our limited knowledge of prevention and treatment therapies. Most emerging infectious diseases originate from pathogen spillovers from wildlife to humans¹. Why are such outbreaks increasing? Does environmental change play a role? It has been

argued that spillovers from wildlife to humans can be enhanced by forest fragmentation, habitat destruction, agricultural expansion, concentrated livestock production, and human penetration in wildlife habitat 2,3,4. However, a quantitative analysis of the nexus between ongoing land use changes and the emergence of new zoonotic diseases is still missing 5,6.

Crucial to understanding the emergence of infectious diseases is the analysis of the factors facilitating the spillover from wildlife prior to further spread within human populations 7,8. In the case of SARS-CoV-2 genomic sequencing has shown that the virus is most closely related (~96%) to a strain present in horseshoe bats⁹. It is still unclear whether the spillover of SARS-CoV-2 occurred directly from bats to humans or through an intermediate species. For instance, a strain of coronavirus very similar to SARS-CoV-2 was detected in Malayan Pangolin (*Manis javanica*)¹⁰, a wild mammal that is frequently illegally smuggled from Southeast Asia into China and sold in markets¹⁰. Regardless of the specific pathway, the pathogen flow of emerging zoonotic diseases to humans is the result of human interactions with wildlife. We argue that the increasing incidence of emerging disease outbreaks is the result of a similar set of drivers able to change the distance and contact rates between wildlife and humans (as well as human-human interaction), including population growth, urbanization, increasing affluence in mid-income countries, and the associated dietary shifts^{11,12,13}. As countries become more affluent demand for animal products increases, leading to an expansion of agriculture and animal husbandry, often at the expense of natural ecosystems¹⁴. For instance, in China the per capita consumption of meat has increased of 20-fold in the last 60 years, which by far exceeds the global average of twofold in the same period^{15,16}. The establishment of intensive animal farming favors the spread of emerging diseases and their transmission to humans 17. Indeed, concentrated livestock production keeps a large number of animals - often immunosuppressed, with low genetic diversity, and in frail health conditions - in close proximity to one another, making them extremely vulnerable to the emergence and spread of epidemics^{3,18,19}. Human penetration in wildlife habitat favors the interaction between humans and wildlife species, either directly through activities like hunting or through other species, particularly livestock that are in closer contact with humans 20,21,22,23. The establishment of pastures, plantations or concentrated livestock farms close to forest margins may increase pathogen flows from wildlife to humans 7,21,23,24,25. Indeed, deforestation and forest fragmentation themselves reshape the dynamics of wildlife communities, possibly leading to the extinction of habitat specialist species, while allowing generalists to thrive 27. Wildlife species that are hosts of pathogens have been found to be relatively more abundant in managed landscapes (e.g., agro-ecosystems and urban areas) than in adjacent undisturbed sites, particularly in the case of bats and other mammal species²⁶.

While several reports in the media have conjectured on a possible link between land use change and the emergence of the COVID19 pandemic, such a hypothesis still has to be supported by a comprehensive high-resolution analysis of land use patterns that combines forest fragmentation to agricultural expansion, livestock production and human encroachment in wildlife habitat 7. Here we analyze environmental and land use changes to explain why China remains at risk for other SARS-related coronavirus outbreaks 1,7 and relate such outbreak risks to ongoing agricultural production trends and dietary shifts. We analyze a set of factors that could make China a suitable location for the spillover to

humans to occur. To that end, while we do not specifically link environmental change or bats as the immediate hosts of the SARS-CoV-2 ancestor^{9,10}, we use horseshoe bats in the genus *Rhinolophus* (family Rhinolophidae) as a model system to understand the risk of future coronavirus outbreaks because China is reported to be a region with both highly diverse horseshoe bats and bat SARS-like CoV ^{28,29,30}.

Results

Among the four CoV genera, two (alpha- and betacoronaviruses) are found in bats. Among the betacoronaviruses, all four subgenera have been discovered in bats, including the SARS-related CoVs (SARSr-CoV, subgenera *Sarbecovirus*)^{28,29,30}. Both SARS-CoV-1 and Swine acute diarrhoea syndrome coronavirus (SADS-CoV) emerged in southeast China and were later detected in horseshoe bats, mainly *Rhinolophus sinicus* and *Rhinolophus affinis*^{9,28,29,30}. Most SARSr-CoVs are detected in horseshoe bats, although some strains have been detected in other genera. SARSr-CoVs in China are most similar to the highly pathogenic human SARS-CoVs^{9,28,29,30}. Therefore, we performed our local analyses of disturbance at bat locations to horseshoe bats in China (Fig 1a; Table S1) and our analyses of disturbance within horseshoe bat distributions in both the larger South, East, and South East Asia region and then China.

Within these distributions we generated 10000 random sampling points (Fig 1a, see SI). Within 30km from every random sampling point we calculate livestock density (n/km^2), forest cover and fragmentation, cropland cover, population density, and the fractional cover of human settlements (see Supplementary Materials). Hotspots were calculated (Fig 1a) using the Getis-Ord algorithm to show the areas with high or low values of land use attributes cluster (Fig 2).

China exhibits a relatively high concentration of livestock production in horseshoe bat distributions (Fig 1a, Table S1). Indeed, China is a hotspot of livestock density within this region (Fig 1b), with statistically significant higher concentrations of chickens, ducks, pigs, goats and cattle (Fig 2a). Within a 30km radius from observed bat locations the density of chicken, ducks, pigs, goats, and cattle was again significantly greater than randomly selected locations. Conversely the sheep density is lower in China, though sheep density was low overall, as it was for other ruminants. The density of chickens, pigs, goats and cattle surrounding (<30km) the points where these bats were recorded and at the randomly selected locations in China within the suitability region were not significantly different, indicating that these random locations have livestock densities that are representative of the areas in which the actual presence of horseshoe bats has been documented.

Forest cover and fragmentation have been related to virus outbreaks from wildlife (including bats) for other zoonotic diseases such as Ebola virus disease². China exhibits on average lower forest cover and cropland density and greater forest fragmentation than the other regions analyzed (Fig 1c). The average forest cover and forest fragmentation in the surroundings (within 30km distance) of random points selected in China and the other regions (Figs 1a, 2b) show that these differences are statistically

significant. Likewise, statistically significant differences (i.e. lower average cover and higher average fragmentation) are found between the points of actual observations of horseshoe bats and randomly selected locations in the regions outside China within the distributions of these bats (Fig 2b).

China also exhibits higher levels of human presence in horseshoe bat distributions, as evidenced by population density and the fraction of the landscape covered by villages, towns, and other human settlement (Fig 2c). Indeed, the region of China suitable for horseshoe bats coincides with hotspots of human settlements (Fig 1d). Collectively, these results demonstrate that China exhibits stronger signs of human encroachment, livestock density, and forest disturbance of SARSr-CoV hosting horseshoe bat distributions than other regions. In China, regions close to forest fragments are more densely used for livestock production and human settlements – and consequently exhibit lower forest and cropland cover (Fig 1b) – thereby favoring the contact between wildlife and humans either directly or through intermediate animals such as livestock. The fact that China is a global hotspot in the concurrence of these three factors (fragmentation, livestock density, and human settlement) is highlighted by the multivariate hotspot analysis (Fig. 3). These three attributes account for bat habitat (fragmentation), livestock, and human presence, which are major factors contributing to the spillover of zoonotic infectious diseases³. Interestingly, we find that China is the global hotspot of simultaneously high forest fragmentation, livestock density and human settlement. The other major global hotspots outside China are found in Java, Bhutan, east Nepal, northern Bangladesh, the Kerala state of India and North-East India, the latter of which are known for past outbreaks of Nipah virus, another bat-related zoonotic disease³¹.

We then use the multivariate hotspot framework to identify regions at high potential risk of SARSr-CoVs spillovers to humans as a result of land use change. To that end the results of the multivariate hotspot analysis were clustered in 30 groups, based on geographic contiguity and similarity in the above three attributes (Fig. 4a; Table S3). We then perturbed one attribute at a time in each group to evaluate that group's susceptibility to transitioning from non-significant conditions (Fig. 3) to a hotspot state (Fig. 4b). This sensitivity analysis (Fig 4b) shows areas at risk of transitioning to hotspots as a result of a future increase in at least one of the analyzed attributes (i.e. forest fragmentation, livestock density, or human settlement). Interestingly the Chinese region south of Shanghai is at high risk of potentially turning into a hotspot as a result of fragmentation increase. Other regions susceptible to hotspot transition as a result of forest fragmentation include Japan and north Philippines. Likewise, the transition region between China's hotspot and Indochina's coldspot and the region surrounding the hotspot of Thailand could turn into hotspots for SARSr-CoV spillover as a result of increasing presence of livestock or humans, respectively (Fig. 4b). These results point both to regions of the world currently suitable for SARSr-CoV spillover from wildlife to humans as well as those at risk of becoming prone to spillover as a result of trajectories of land use change and human penetration (Fig. 4c; Fig.S8 SI)

Discussion

Food systems are often related to human health via the impact of unhealthy diets on the emergence of chronic diseases such as type 2 diabetes and cardiovascular syndromes. However, they can also affect human health more indirectly, through land use changes induced by the increasing demand for food commodities such as meat or other animal products, a phenomenon known as “the livestock revolution”¹⁷. In many regions of the world the growth in livestock production has often led to the expansion of agriculture, forest destruction, and the encroachment of cropland and concentrated livestock farms into disturbed wildlife habitat¹⁴. This study connected the dots between the emergence of SARSr-CoV epidemics and land use changes resulting from both intensive farming and agricultural expansion. Our approach uses the horseshoe bats as a model family because of their key role as hosts of *Sarbecovirus* coronaviruses, which have caused SARS, COVID-19, and SARS2,9,25,27,28,29,30. Other strains of related viruses have been found in other bat genera, but these relationships are less clear^{28,29,30}. The widespread sampling of other bats may find species-specific relationships, though horseshoe bats appear to be the reservoirs where most SARSr-CoVs have their evolutionary ancestors so we assume they are the most appropriate model. The risk to humans from other coronaviruses, therefore, will be different, because their host distributions are different, and two CoV genera (gamma- and delta-coronaviruses) are mostly bird viruses.

The bat location data and species distribution data also suffer from different, but related issues. The bat location data are presence only data. True absence data are difficult to obtain, therefore we randomly sampled within different locations to generate pseudo-absence data. Choosing where to sample from also present difficulties, so we chose horseshoe bat distribution data for species that existed within China, East Asia, South, and South East Asia. This presents further issues as the distribution of one species, the greater horseshoe bat (*Rhinolophus ferrumequinum*), extends from Western Europe, Northern Africa, Central Asia and Eastern Asia. We therefore weighted our sampling based on the number of overlapping species distributions to account for this. However, these species distributions are large polygons and the realized niches used within them by the species likely differ, so better niche models using presence and, ideally, presence/absence data are required to develop better species presence predictions³³. However, our results for random locations in China and outside China and reported bat observations were comparable.

More generally, though using the relatively specific bat and virus relationships, we took a high-level approach to understand the more distal or ultimate (rather than proximal) causes of infectious disease emergence in China, linking environmental change and human drivers like agricultural intensification. Different infectious diseases have different transmission mechanisms and life cycles, and not all will respond to such changes in the same way. For example, directly transmitted, acute infections with short incubation and infectious periods, like SARSr-CoVs, will likely be dependent on hosts having greater densities, like in China, for them to emerge. The epidemic potential is then also increased through local and global movement and trade, either of people, wildlife, or livestock^{20,34,35,36}. Along with the biological properties of the virus and hosts, the true risk of both the initial cross-species transmission and epidemic potential is either increased or limited by more proximal mechanisms, such as biosecurity, health and safety measures (e.g. personal protective equipment, meat hygiene) that can reduce risk, even

if the ultimate factors are present and increasing through the processes of habitat fragmentation and human encroachment^{20,2}.

Spillover of infectious disease such as SARS, COVID-19 and SADS from wildlife to humans likely requires the coexistence of horseshoe bats and humans in the same environment and is favored by the presence of intermediate animal species, particularly livestock because it is in closer contact with humans. The fragmentation and disturbance of forest ecosystems likely favors habitat generalist bat species. In particular, chickens, ducks, and pigs have been associated with the spread of several zoonotic viral infections, such as influenza viruses. This study demonstrates that in China these important factors responsible for reducing the distance between wildlife and humans co-occur both in horseshoe bat distributions and in the surroundings of actual documented bat occurrence. These results are consistent with the notion that population growth and increasing meat consumption associated with urbanization and economic growth have expanded the footprint of agriculture, leading to human encroachment in wildlife habitat and increased livestock density in areas adjacent to fragmented forest patches. China has dramatically increased animal consumption³⁷, likely as the result of increasing affluence. In China, meat supply is largely reliant on domestic production using imported feed (e.g. soy from the Americas)³⁷, which explains the high livestock density in many rural areas, including those at the forest margins. Likewise, economic growth and the shift to diets richer in animal products explains the increasing demand for wild animal meat delicacies, increasing human-wildlife interactions through multiple pathways and the disturbance of forest habitat in more remote locations – frequently abroad – through trade-related teleconnections³⁸.

The multivariate hotspot analysis highlights how China is the largest hotspot for the concurrence of high forest fragmentation, livestock density, and human presence in our analysis (Fig. 3). The sensitivity analyses identifying the possible transition to new hotspots in response to an increase in one of these attributes (Fig. 4b) highlights areas that could become suitable for spillover and the type of land use change that could induce hotspot activation. Therefore, this analysis highlights region-specific targeted interventions that are urgently needed to increase resilience to SARSr-CoV spillovers. For instance, the green dots in Fig. 4 could be turned into hotspots as a result of forest fragmentation. In these regions resilience can be built through forest conservation or restoration efforts. Indeed, land use change evaluations should consider the risk of activating new hotspots suitable for wildlife-to-human spillover of pathogens such as SARSr-CoV, an aspect that has seldom been included in the impact analysis of land use change. Likewise, other regions such as the China-Indochina transition zone or central Thailand are prone to hotspot transitioning as a result of increased livestock density of urbanization, respectively. In these cases, mitigation of SARSr-CoV emergence can be enhanced by reducing livestock or human density, respectively, thereby inverting ongoing dietary and urbanization trends. Thus, environmental health, is tightly connected to both animal and human health, as recently stressed by planetary and 'one health' discourses, which advocate for more holistic views of global health, encompassing environment, animals, and people as well as their interactions³⁹.

Materials And Methods

Bat location data

Most SARS-related CoVs are detected in horseshoe bats, although some strains have also been detected in other genera^{35,40,41,42,43,44,45,46}. SARSr-CoVs in China are most similar to the highly pathogenic human SARS-CoVs^{47,48,49}.

We restricted our local analyses of disturbance at bat locations to Rhinolophid bats in China. We performed a Web of Science® search on 10/04/2020 using the following Boolean Operators: Rhinoloph* AND China AND Monitor* OR Survey OR Niche OR Distribution. We found 129 unique references. We removed all those published before 2000, reporting data outside China, review articles, and non-English (specifically 23 Chinese language publication), those with no Rhinolophid data, and those reporting only fossil records. We kept infection studies. This left 48 publications. We then further manually reviewed the publications for those reporting location data³⁵ but more specifically those with latitude and longitude, leaving 17 publications and 264 observations (see Fig. 1a; Table S1).

Bat distribution data

We restricted our analyses of disturbance in bat distributions to Rhinolophid bats in both the larger South, East and South East Asia region (but see main manuscript) and then China. We searched the IUCN Red List database (<https://www.iucnredlist.org/search>) using Taxonomy: Rhinolophidae and Region: East Asia and South & South East Asia (herein 'regional') followed by Taxonomy: Rhinolophidae and Region: East Asia: China, Hong Kong & Taiwan (herein 'Chinese') classifications and downloaded the shapefiles for the 55 regional and 22 Chinese Rhinolophus species present in the region. We consider these areas as regions of suitable habitat for Rhinolophidae. The extent of this study area exceeds 28.5 million km².

Within these putative species distributions, we generated 10000 random sampling points with a local sampling density that is proportional to the number of species whose distributions were reported at the point. For every random sampling points we consider a circular area of 30km radius within which we calculate livestock density, forest cover and fragmentation, cropland cover, population density and the fractional cover of human settlements as explained below. The average values of these statistics are then calculated for China and the other regions of the world with habitat suitable for Rhinolophidae and compared and the difference is tested for significance using the Mann-Whitney non-parametric test in Mathematica®.

Livestock, forest cover, and population data

We took livestock data from the GeoWiki database that provides georeferenced livestock counts (in heads/km²) at 1 km resolution for chickens, ducks, pigs, goats, sheep, and cattle (<https://livestock.geowiki.org/home-2/>). We quantified human presence both in terms of population density at 1 km resolution and as fraction of the landscape taken by villages, towns or other settlements from the WorldPop

database at 1 km resolution. We used cropland data (at 30×30m² resolution) from 50. Forest cover data are available at 30m resolution annually between 2000 and 2018⁵¹. Forest cover is associated with the presence of trees taller than 5 m. Forest loss or gain was determined as the difference in forest cover between these two years.

Forest fragmentation analyses

We performed a forest fragmentation analyses based on Vogt et al.⁵² using the 30m forest cover data. This method distinguishes forest cores, from forest margins and patches. Every 30m pixel is classified as wooded or non-wooded, based on whether its tree cover was greater or smaller than 50% in the year 2018. Forest cores are wooded pixels that are not adjacent to non-wooded pixels. Conversely, forest patches are made of wooded pixels that are not adjacent to forest core pixels. Wooded pixels that are neither core nor patch pixels occur at the margins of forest cores. Forest fragmentation was then quantified in terms of a composite fragmentation index (CFI)², defined as the ratio between the sum of number of pixels classified as “margins”, “patches”, or smaller core areas (i.e., <200 ha), and the total number of pixels (wooded + non-wooded) in the 30km circles used to characterize land cover and land use in the surroundings of the points of actual bat observations or the randomly generated points. This index ranges between 0 and 1.

Hotspot Analyses and multivariate clustering

We mapped statistically significant hotspots of livestock density, forest fragmentation, and human settlements. To be a hotspot, an area needs to have a high (or low, in the case of cold-spots) value of its attribute and be also surrounded by other areas with high (or low) values of the same attribute. To that end, the 30km circles centered on the 10000 random points (Fig. 1a) considered in this study were used to carry out a hotspot analysis applying the Getis-Ord algorithm (Gi* statistics). The Gi* statistic shows to what extent areas with high or low values tend to cluster thereby forming a hotspot. The result of the Gi* analysis is reported in terms of statistical significance with 90%, 95%, and 99% confidence (Fig. 1).

We then used two different methods to generate a multivariate distribution for the three indicators (livestock density, forest fragmentation and human settlements). First, we averaged their Gi*. Since the Gi* is a z-score, i.e. it has a standard normal distribution, a linear combination of the three Gi* indicators, such as their average, is a standard normal distribution and can still be represented with the same significance levels (Fig. 2). Second, we performed a spatially constrained multivariate clustering analysis. A Minimum Spanning Tree (MST) from the connectivity graph of the features was built, and then the SKATER (Spatial “K”luster Analysis by Tree Edge Removal) clustering method was used⁵³. The SKATER iteratively cuts branches in the MST, based on data variability among and within groups and on a spatial constraint, until it reaches the user-defined number of groups. The spatial constraint defined here is a k nearest neighbors type with 8 neighbors, meaning each feature in a group must have at least one of its 8 nearest neighbors in the same group. We chose 30 as the number of groups, calculated a set of summary statistics and boxplots for the groups and compared them to their global values (Table S2). For each

indicator, we calculated the R^2 value as the reduction in variance of the indicator obtained by grouping, divided by the original variance of the indicator (Table S2). While the modularity analysis based on pseudo F-statistics shows that the optimal number of groups (the maximum differences between groups while maximizing within group similarity) is 12, here we studied 30 groups to analyse distinct regional patterns. Having a greater number of groups allows us to identify groups that are susceptible to transitioning to a hotspot because they are not “too different” from hotspots.

Declarations

Competing interest statement

The authors declare no competing interests.

Author contributions

M.C.R. designed research; M.C.R. and D.T.S.H performed research; M.C.R., P.D. and N.G. analyzed data; P.D., M.C.R. and D.T.S.H wrote the paper.

Acknowledgments

M.C.R and N.G. are supported by ENI Enrico Mattei Foundation (FEEM) and by Cariplo Foundation (SusFeed project 0737 CUP D49H170000300007). D.T.H. is supported by USDA Hatch Multistate project no. W4190 capacity fund; Rutherford Discovery Fellowship RDF-MAU1701.

References

1. Jones, K. E. *et al.* Global trends in emerging infectious diseases. *Nature* **451**, 990-993 (2008).
2. Rulli, M. C., Santini, M., Hayman, D. T. & D’Odorico, P. The nexus between forest fragmentation in Africa and Ebola virus disease outbreaks. *Scientific reports* **7**, 41613 (2017).
3. Espinosa, R., Tago, D. & Treich, N. Infectious Diseases and Meat Production. *Environ Resource Econ* (2020).
4. Young, H., Griffin, R. H., Wood, C. L. & Nunn, C. L. Does habitat disturbance increase infectious disease risk for primates? *Ecol. Lett.* **16**, 656–663 (2013).
5. Rohr *et al.* Emerging human infectious diseases and the links to global food production. *Nat Sustain* **2**(6):445–456, (2019).
6. Gottdenker, N. L., Streicker, D. G., Faust, C. L. & Carroll, C. R. Anthropogenic land use change and infectious diseases: a review of the evidence. *EcoHealth* **11**, 619–632 (2014).
7. Allen T. *et al.*, Global hotspots and correlates of emerging zoonotic diseases, *Nature Coomunications*, **8**: 1124, (2017).
8. Wu et al., Economic growth, urbanization, globalization, and the risks of emerging infectious diseases in China: A review, *Ambio*, **46**:18–29 (2017).

9. Zhou, P. *et al.* A pneumonia outbreak associated with a new coronavirus of probable bat origin. *Nature* **579**, 270-273, (2020).
10. Lam, T. T. *et al.* Identifying SARS-CoV-2 related coronaviruses in Malayan pangolins. *Nature*, (2020).
11. Tilman, D. & Clark, M. Global diets link environmental sustainability and human health. *Nature* **515**, 518-522 (2014).
12. Hassell, J. M., Begon, M., Ward, M. J. & Fèvre, E. M. Urbanization and disease emergence: dynamics at the wildlife–livestock-human interface. *Trends Ecol. Evol.* 32, 55–67 (2017).
13. Shah, H. A., Huxley, P., Elmes, J. & Murray, K. A. Agricultural land-uses consistently exacerbate infectious disease risks in Southeast Asia. *Nat. Commun.* 10, 4299 (2019).
14. Naylor, R. Expanding the boundaries of agricultural development. *Food Security* **3**, 233 (2011).
15. FAO, 2017. FAOSTAT. Food and Agriculture Organization of the United Nations, Rome, Italy
16. Godfray, H.C.J., *et al.* Meat consumption, health, and the environment. *Science*, 361, eaam532430026199 (2018).
17. Delgado, C., Rosegrant, M., Steinfeld, H., Ehui, S. & Courbois, C. , Livestock to 2020: The next food revolution. *Food, Agriculture, and the Environment Discussion Paper 28*, International Food Policy Research Institute, Washington, DC, (1999).
18. Coker, R. *et al.* Towards a conceptual framework to support one-health research for policy on emerging zoonoses. *Lancet Infect Dis* 11:P326–P331 (2011).
19. Civitello, D.J. *et al.* Biodiversity inhibits parasites: broad evidence for the dilution effect. *Proc Natl Acad Sci* 112(28):8667–8671 (2015).
20. Wilkinson, D. A., Marshall, J. C., French, N. P. & Hayman, D. T. Habitat fragmentation, biodiversity loss and the risk of novel infectious disease emergence. *Journal of the Royal Society Interface* **15**, 20180403 (2018).
21. Johnson, C. K. *et al.* Global shifts in mammalian population trends reveal key predictors of virus spillover risk. *Proceedings of the Royal Society B* **287** (2020).
22. Bloomfield, L. S. P., McIntosh, T. L. & Lambin, E. F. Habitat fragmentation, livelihood behaviors, and contact between people and nonhuman primates in Africa. *Landscape Ecology* **35**, 985-1000, doi:10.1007/s10980-020-00995-w (2020).
23. Pulliam, J. R. *et al.* Agricultural intensification, priming for persistence and the emergence of Nipah virus: a lethal bat-borne zoonosis. *Journal of the Royal Society Interface* **9**, 89-101 (2012).
24. Chua, K. B. *et al.* Fatal encephalitis due to Nipah virus among pig-farmers in Malaysia. *The Lancet* **354**, 1257-1259 (1999).
25. Zhou, P. *et al.* Fatal swine acute diarrhoea syndrome caused by an HKU2-related coronavirus of bat origin. *Nature* **555**, 255-258(2018).
26. Gibb, R., *et al.* Zoonotic host diversity increases in human-dominated ecosystems. *Nature* **584**, 398–402 (2020).

27. Meyer, C. F., Struebig, M. J. & Willig, M. R. in *Bats in the anthropocene: Conservation of bats in a changing world* 63-103 (Springer, Cham, 2016).
28. Cui, J., Li, F. & Shi, Z. Origin and evolution of pathogenic coronaviruses. *Nature Reviews: Microbiology* **17**, 181-192(2019).
29. Fan, Y., Zhao, K., Shi, Z. & Zhou, P. Bat coronaviruses in China. *Viruses* **11**, 1-11, (2019).
30. Wong, A. C. P., Li, X., Lau, S. K. P. & Woo, P. C. Y. Global epidemiology of bat coronaviruses. *Viruses* **11**, doi:10.3390/v11020174 (2019).
31. Soman Pillai V, Krishna G, Valiya Veetil M. Nipah Virus: Past Outbreaks and Future Containment. *Viruses*. **12**(4):465 (2020).
32. Naylor, R. (2011). Expanding the boundaries of agricultural development. *Food Security*, 3(2), 233. <https://doi.org/10.1007/s12571-011-0123-6>
33. Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M. B. BIOMOD—a platform for ensemble forecasting of species distributions. *Ecography* **32**, 369-373 (2009).
34. Chinazzi, M. *et al.* The effect of travel restrictions on the spread of the 2019 novel coronavirus (COVID-19) outbreak. *Science* **368**, 395-400 (2020).
35. Kraemer, M. U. G. *et al.* The effect of human mobility and control measures on the COVID-19 epidemic in China. *Science* **368**, 493-497 (2020).
36. Yang, Q. *et al.* Assessing the role of live poultry trade in community-structured transmission of avian influenza in China. *Proceedings of the National Academy of Sciences* **117**, 5949-5954 (2020).
37. D'Odorico, P., *et al.* The global food-energy-water nexus. *Reviews of Geophysics*, **56**, 456–531 (2018).
38. Meyfroidt, P., Lambin, E. F., Erb, K. H., & Hertel, T. W. Globalization of land use: Distant drivers of land change and geographic displacement of land use. *Current Opinion in Environmental Sustainability*, **5**(5), 438–444 (2013).
39. Whitmee, S. *et al.* Safeguarding human health in the Anthropocene epoch: report of The Rockefeller Foundation–Lancet Commission on planetary health. *The Lancet* **386**, 1973-2028 (2015).
40. Woo, P.C.; *et al.* Discovery of seven novel Mammalian and avian coronaviruses in the genus deltacoronavirus supports bat coronaviruses as the gene source of alphacoronavirus and betacoronavirus and avian coronaviruses as the gene source of gammacoronavirus and deltacoronavirus. *Virology*, **86**, 3995–4008, (2012).
41. Corman, V.M.; *et al.* Rooting the Phylogenetic Tree of Middle East Respiratory Syndrome Coronavirus by Characterization of a Conspecific Virus from an African Bat. *Virology*, **88**, 11297–11303, (2014).
42. ICTV 2018: Coronidovirinae. Available online: https://talk.ictvonline.org/taxonomy/p/taxonomy-history?taxnode_id=20186105 (2018).
43. Huang, C.; *et al.* A Bat-Derived Putative Cross-Family Recombinant Coronavirus with a Reovirus Gene. *PLoS Pathog*, **12**, e1005883 (2016).
44. Woo, P.C.; *et al.* Comparative analysis of twelve genomes of three novel group 2c and group 2d coronaviruses reveals unique group and subgroup features. *Virology*, **81**, 1574–1585, (2007).

45. Lau, S.K.P.; *et al.* Receptor Usage of a Novel Bat Lineage C Betacoronavirus Reveals Evolution of Middle East Respiratory Syndrome-Related Coronavirus Spike Proteins for Human Dipeptidyl Peptidase 4 Binding. *Infect. Dis.*, **218**, 197–207 (2018).
46. Lau, S.K.; *et al.* Severe acute respiratory syndrome coronavirus-like virus in Chinese horseshoe bats. *Natl. Acad. Sci. USA*, **102**, 14040–14045 (2005).
47. Hu, B.; *et al.* Discovery of a rich gene pool of bat SARS-related coronaviruses provides new insights into the origin of SARS coronavirus. *PLoS Pathog.*, **13**, e1006698 (2017).
48. Andersen KG, Rambaut A, Lipkin WI, Holmes EC & Garry RF. The proximal origin of SARS-CoV-2. *Nature medicine*. **26**(4):450-452 (2020).
49. Lee, S.; *et al.* Genetic Characteristics of Coronaviruses from Korean Bats in 2016. *Ecol.*, **75**, 174–182, (2018).
50. Teluguntla, P., *et al.* Global Cropland Area Database (GCAD) derived from Remote Sensing in Support of Food Security in the Twenty-first Century: Current Achievements and Future Possibilities. Chapter 7, Vol. II. Land Resources: Monitoring, Modelling, and Mapping, Remote Sensing Handbook edited by Prasad S. Thenkabail (2014).
51. Hansen MC, *et al.* High-resolution global maps of 21st-century forest cover change. *Science*, **342**:850–853 (2013).
52. Vogt, P., Riitters, K. H., Estreguil, C. J., Kozak, T. G. & Wade, J. D. Wickham Mapping spatial patterns with morphological image processing. *Landscape Ecol.* **22**, 171–177 (2007).
53. Assuncao, R.M., Neves, M. C., Camara, G., & Da Costa Freitas, C., Efficient Regionalisation Techniques for Socio-economic Geographical Units using Minimum Spanning Trees. *International Journal of Geographical Information Science* **20** (7): 797–811 (2006).

Figures

Figure 1

Univariate spatial analysis of coronavirus outbreak drivers (A) Sampling points randomly generated within China (dark purple) and outside China (light purple) and bat location points (yellow), weighted by the horseshoe bat species distributions present in East, South & South East Asia; (B) hotspots (red) and coldspots (blue) of livestock density; (C) hotspots of forest fragmentation; (D) hotspots of human settlement. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

Distribution comparison for coronavirus outbreak drivers. Average distributions of livestock (A), land cover and use (B), and human population (C) in areas likely suitable for horseshoe bat occurrence in China and in the rest of their distribution. Error bars correspond to the 20% and 80% percentiles. Different capital letters indicate statistically different means ($\alpha=0.05$).

Figure 3

Multivariate spatial analysis of coronavirus outbreak drivers. Hotspot analysis based on the average G_i^* Z-Score values for fragmentation, livestock density, and human settlements. Hotspots are classified based on their significance level. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 4

Multivariate grouping analysis of coronavirus spillover drivers. (A) Multivariate groups analysis based on fragmentation, livestock and settlements attributes; (B) Areas at risk of becoming hotspots as a result of changes in forest fragmentation (green), increase in livestock density (fuchsia) and human settlement (purple); (C) Possible trajectories of hotspot transition. These 3 groups represent areas not yet classified as hotspots (not significant by Gettis Ord analysis), but which may change trajectory. The solid triangle

represents the safe space of variation for the 3 indicators (using multivariate Getis-Ord analysis). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterials.pdf](#)