

The coevolutionary mosaic of bat-betacoronaviruses spillover risk

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Driven by the need to understand the ecological factors involved in the emergence of betacoronavirus through bat hosts, we develop an approach to the assessment of spillover risk based on the Geographic Mosaic Theory of Coevolution. In doing so, we provide a global mapping of the risk posed by viruses, reflecting the fact that this risk has many ecological and evolutionary origins. Our framework reveals that reservoir richness alone is not a sufficient predictor of risk, and offers alternative insights based on viral sharing, host compositional uniqueness, and host phylogenetic diversity. By comparing our aggregated measure of risk to a proxy for human density, namely the proportion of each pixel that is covered by urban or built land, we provide a synthetic risk map, allowing the identification of hotspots where the bat-betacoronavirus system may originate novel viruses in humans.

Keywords:

bats
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disease ecology
geographic mosaic theory of coevolution
phylogenetic diversity
viral sharing
SARS-CoV-2

Spillover risk is not unidimensional. From the standpoint of an animal community, *i.e.* a pool of suitable hosts, it is driven by a multiplicity of factors (Plowright et al. 2017). The global richness of hosts is one such component commonly mentioned/analysed (see *e.g.* Anthony et al. 2017 for coronaviruses), but there is an argument to be made that species who are not competent (or know) hosts of a specific virus genus may not factor into this (Plowright et al. 2015), or that species who are assumed to share viruses at different rates should be weighted accordingly (Albery et al. 2020). In mammals, key functional traits (for which phylogeny is a reasonable proxy) are determinants of the spillover potential (Olival et al. 2017); these include, notably, body mass and affinity for urban environments (Albery et al. 2022). Finally, especially when the pool of potential hosts spans the entire globe, there may be local host pools that are highly unique; not having been observed in other locations, these can act on the overall risk either by providing novel contact opportunities, reflecting unique host-environment combinations (Engering et al. 2013), or facilitating rapid evolutionary changes in specialism of their pathogens (Agosta et al. 2010). In the specific case of generalist pathogens, there is conceptual and empirical support to the idea that these community- level mechanisms are even more important in driving the overall risk (Power and Mitchell 2004).

Bats are important reservoir hosts for different classes of microorganisms (Chu 2008, Donaldson 2010, Li 2010), some of which can threaten human health. Chiropterans emerged around 64 million years ago and are one of the most diverse mammalian orders, with an estimated richness of more than 14000 species (Peixoto et al. 2018, Simmons and Cirranello 2020). They exhibit a broad variety of habitat use, behaviour, and feeding strategies, resulting in their playing an essential role in the delivery of several ecosystem services tied to important ecosystem-derived benefits (Kasso and Balakrishnan 2013). For example, over two-thirds of bats are known to be either obligate or facultative insectivorous mammals, therefore playing an important role in the regulation of insect pests that can affect crops (Williams-Guillén et al. 2008, Voigt and Kingston 2016), and vectors of diseases that put a risk on human health

(Gonsalves et al. 2013a, b). Because bats are globally distributed and have a long evolutionary history, phylogeographic and biogeographic approaches are required to shed light on the extant distribution of coevolutionary processes between bats and the pathogens they carry. Not all areas in which bats, viruses, and human are co-occurring are facing a risk of spillover towards human populations, and the areas in which this risk exist may not be facing risks of the same nature and magnitude.

In this paper, we examine the biogeographic structure of bats-betacoronaviruses associations, based on a curated dataset of known and recently discovered hosts. This work is important both as a description of the bats-betacoronavirus complex, but also because more broadly, bats are known reservoirs for a variety of emerging viruses and pathogens (Calisher et al. 2006, Melaun et al. 2014), making balancing the needs for bat conservation and disease prevention a potentially difficult act and a source of human-wildlife conflicts, especially in more densely populated areas (Stone et al. 2015, Rego et al. 2015). By drawing on concepts from the Geographic Mosaic Theory of Coevolution (Thompson 2005), we turn these associations into a spatially explicit additive mapping of zoonotic risk components, which reveals extreme heterogeneity of risk at the global scale; furthermore, we identify the Amazon and South-Eastern Asia as hotspots of phylogenetic distinctiveness of betacoronaviruses (Anthony et al. 2017); surprisingly, current data suggest that viral sharing between hosts is high in the Amazon and low in South-Eastern Asia, which has the potential to result in different evolutionary dynamics between these two regions.

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Methods

1.1. Known betacoronavirus hosts We downloaded the data on bats hosts of betacoronaviruses assembled by Becker et al. (2022) from <https://www.viralemergence.org/betacov> on Apr. 2022, and filtered it to “known” hosts (established before the emergence of SARS-CoV-2) and “novel” hosts (confirmed through sampling since the emergence of SARS-CoV-2). The original database was assembled by a combination of data mining and literature surveys, including automated alerts on the “bats” and “coronavirus” keywords to identify novel empirical evidence of bats-betacoronaviruses associations.

1.2. Bats occurrences We downloaded the rangemap of every extant bat species that was either classified as an empirically documented host of beta-coronaviruses from the previous step, according to recent IUCN data (IUCN 2021). The range maps were subsequently rasterized using the rasterize function from GDAL (Rouault et al. 2022) at a resolution of approximately **TK TP**. For every pixel in the resulting raster where at least one bat host of betacoronavirus was present, we extract the species pool (list of all bat species), which was used to calculate the following risk assessment components: phylogenetic diversity, bat compositional uniqueness, and predicted viral sharing risk.

1.3. Bats phylogeography For every pixel, we measured Faith’s Phylogenetic Diversity (Faith 1992) based on a recent synthetic tree with robust time calibration, covering about 6000 mammalian species (Upham et al. 2019). Faith’s PD measures the sum of unique branches from an arbitrary root to a set of tips, and comparatively larger values indicate a more phylogenetic diverse species pool. We measured phylogenetic diversity starting from the root of the entire tree (and not from Chiroptera); this bears no consequences on the resulting values, since all branches leading up to Chiroptera are only counted one per species pool, and (as we explain when describing the assembly of the composite risk map), all individual risk components are ranged in [0,1]. This measure incorporates a richness component, which we chose not to correct for; the interpretation of the phylogenetic diversity is therefore a weighted species richness, that accounts for phylogenetic over/under-dispersal in some places.

1.4. Bats compositional uniqueness For every species pool, we measured its Local Contribution to Beta-Diversity (Legendre and De Cáceres 2013); LCBD works from a species-data matrix (traditionally noted as **Y**), where species are rows and sites are columns, and a value of 1 indicates occurrence. We extracted the **Y** matrix assuming that every pixel represents a unique location, and following best practices (Legendre and Condit 2019) transformed it using Hellinger’s distance to account for unequal bat richness at different pixels. The correction of raw community data is particularly important for two reasons: first, it prevents the artifact of richer sites having higher importance; second, it removes the

effect of overall species richness, which is already incorporated in the phylogenetic diversity component. High values of LCBD indicate that the pixel has a community that is on average more dissimilar in species composition than what is expected knowing the entire matrix, i.e. a more unique community. Recent results by Dansereau et al. (2022) shows that LCBD measures are robust with regards to spatial scale, and are therefore applicable at the global scale.

1.5. Viral sharing between hosts For all bat hosts of betacoronaviruses, we extracted their predicted viral sharing network (Albery et al. 2020). This network stores pairwise values of viral community similarity. To project viral sharing values into a single value for every pixel, we averaged the pairwise scores. High values of the average sharing propensity means that this specific extant bat assemblage is likely to be proficient at exchanging viruses.

1.6. Composite risk map To visualize the aggregated risk at the global scale, we combine the three individual risk components (phylogenetic diversity, compositional uniqueness, and viral sharing) using an additive color model (Seekell et al. 2018). In this approach, every risk component gets assigned a component in the RGB color model (phylogenetic diversity is green, compositional uniqueness is red, and viral sharing is blue). In order to achieve a valid RGB measure, all components are re-scaled to the [0,1] interval, so that a pixel with no sharing, no phylogenetic diversity, and no compositional uniqueness is black, and a pixel with maximal values for each is white. This additive model conveys both the intensity of the overall risk, but also the nature of the risk as colors diverge towards combinations of values for three risk components. Out of the possible combinations, the most risky in terms of rapid diversification and spillover potential is high phylogenetic diversity and low viral sharing (Gomulkiewicz et al. 2000, Cavender-Bares et al. 2009), in that this allows multiple independent host-virus coevolutionary dynamics to take place in the same location. In the colorimetric space, this correspond to yellow – because the HSV space is more amenable to calculations for feature extraction (see e.g. Keke et al. 2010), we measured the risk level by calculating the angular distance of the hue of each pixel to a reference value of 60, and weighted this risk level by the value component. Specifically, given a pixel with colorimetric coordinates (h, s, v) , its ranged weighted risk value is

$$v \times \left[1 - \frac{|\text{atan}(\cos(\text{rad}(h)), \sin(\text{rad}(h))) - X|}{2\pi} \right],$$

where X is $\text{atan}(\cos(\text{rad}(60)), \sin(\text{rad}(60)))$, a constant approximately equal to 0.5235.

1.7. Viral phyogeography and evolutionary diversification We used the following query to pull all betacoronavirus sequence data from the GenBank Nucleotide database except SARS-CoV-2; (“Betacoronavirus”[Organism] OR betacoronavirus[All Fields]) NOT (“Severe acute respiratory syndrome coronavirus 2”[Organism] OR sars-cov-2[All Fields]). We added a single representative sequence for SARS-CoV-2 and manually curated to remove sequences without the RNA-dependent RNA polymerase (RdRp) sequence or that contained words indicating recombinant or laboratory strains including “patent,” “mutant,” “GFP,” and “recombinant.” We filtered over-represented taxa including betacoronavirus 1, hCoV-OC43, Middle East respiratory syndrome coronavirus, Murine hepatitis virus, and hCoV-HKU1. Curated betacoronavirus RdRp sequences were then aligned using MAFFT v 1.4.0 (**Katoh and Standley 2013**, parameters in text?) and a maximum likelihood tree reconstructed in IQ-TREE v 1.6.12 (Nguyen et al. 2015) with ModelFinder (Kalyaanamoorthy et al. 2017) ultrafast bootstrap approximation (Hoang et al. 2018) and the following parameters (**STEPH WILL ADD**, parameters in text?).

We first tested the hypothesis that hotspots of viral diversification would track hotspots of bat diversification. To do so, we plotted the number of known bat hosts (specifically only those included in the phylogeny, so there was a 1:1 correspondence between data sources) against the “mean evolutionary distinctiveness” of the associated viruses. To calculate this, we derived the fair proportions evolutionary distinctiveness (Isaac et al. 2007) for each of the viruses in the tree, then averaged these at the bat species level, projected these values onto their geographic distributions, and averaged across every bat found in a given pixel. As such, this can be thought of as a map of the mean evolutionary distinctiveness of the known viral community believed to be associated with a particular subset of bats present.

1.8. Co-distribution of hosts and viral hotspots Subsequently, we tested the hypothesis that the biogeography of bat betacoronaviruses should track the biogeography of their hosts. To test this idea,

we loosely adapted a method from (Kreft and Jetz 2007, 2010), who proposed a phylogenetic method for the delineation of animal biogeographic regions. In their original method, a distance matrix - where each row or column represents a geographic raster's grid cell, and the dissimilarity values are the “beta diversity similarity” of their community assemble - undergoes non-metric multidimensional scaling (NMDS); the first two axes of the NMDS are projected geographically using a four-color bivariate map. Here, we build on this idea with an entirely novel methodology. First, we measure the phylogenetic distance between the different viruses in the betacoronavirus tree by using the cophenetic function in ape (Paradis and Schliep 2019); subsequently, we take a principal components analysis of that distance matrix (readily interchangeable for NMDS in this case) to project the viral tree into an n-dimensional space. We then take the first two principal components and, as with the evolutionary distinctiveness analysis, aggregated these to a mean host value and projected them using a four-color bivariate map.

2

Results and discussion

2.1. Host richness does not predict virus distinctiveness Bats are found worldwide and are both one of the most diverse groups among mammals (**Moratelli & Calisher, 2015**), and one of the main animal reservoir for different strains of betacoronaviruses (Drexler et al. 2014). This has attracted attention to areas where high diversity of bats, and therefore presumably high diversity of betacoronaviruses, can be an important issue for human health (Calisher et al. 2006, Moratelli and Calisher 2015). By overlaying the IUCN rangempas for confirmed bat hosts of betacoronaviruses [fig. 1; top], we see that the main hotspots of host richness are primarily South-Eastern Asia, parts of Southern Europe, and to a lesser extent parts of Africa in the -25-0 range of latitudes. The description of host richness is an important first step towards understanding risk, as previous research (**Anthony et al., 2017; Mollentze & Streicker, 2020**) states that locally diverse bat communities could maintain more viruses and hence, a higher probability of having a pathogen that could represent a risk for human health.

Nevertheless, locally diverse and virus-rich bat communities could represent an increased risk of spillover under climate change through the creation of novel interactions (**Ice ice berg berg**), and therefore the diversity of betacoronavirus strains should similarly be accounted for. In fig. 1 (bottom), we contrast the evolutionary distinctiveness of bats and viruses – this reveals a slightly different portrait than bat richness alone. Chiropterans can be classified, from a macro-evolutionary standpoint, as microchiroptera and macrochiroptera, where macrochiroptera have an older history from an evolutionary perspective compared to macrochiroptera (Teeling et al. 2005, Springer 2013). Specifically, we would expect that the so-called “New World” group of bats, being more evolutionary distinct, would also have evolutionary distinct viruses. Indeed fig. 1 (bottom) reveals it to be the case, and this region harbors a distinct bat-betacoronavirus complex. By contrast, South-Eastern Asia has a lot of non-evolutionary distinct bats, but evolutionary-distinct viruses.

It is noteworthy that outside of South America, viral evolutionary distinctiveness does not accurately tracks host diversity, with some areas having over-distinct viruses (southern China but, oddly, not the rest of southeast Asia). There are a number of likely explanations. First, given the richness of bats in southeast Asia, many betacoronaviruses likely remain to be discovered in this region. Indeed, global predictions by (**Becker?**) highlight that southeast Asia is a likely hotspot of unconfirmed hosts of betacoronaviruses, which would likely result in additional viral discoveries. This idea is unsurprising given the growing realization, around the emergence of SARS-CoV-2, that a unique lineage of similar viruses are widespread in bats but still mostly undescribed. The most distinct bats/betacoronavirus complex is found in South America, a region with a comparatively lower number of hosts; this matches with the isolation through variance of the host group, and may highlight a different co-evolutionary dynamic. Alternatively, this distinctiveness hotspot may be a product of under-sampling: South-America is one of the places where the fewest betacoronaviruses have been discovered (Anthony et al. 2017, Olival et al. 2017, Allen et al. 2017), resulting in sparser phylogenetic tree, thereby artificially inflating distinctiveness. Adding more viruses would bring the distinctiveness of known sequences down.

2.2. The phylogeographic regions of hosts and their viruses overlap Despite the difference in evolutionary distinctiveness globally, there are reasons to expect that the phylogeography of bats and betacoronaviruses should show some degree of congruence. High density of hosts sharing the same virus (albeit possibly different strains) can drive or result from evolution of the bat antiviral immune system, resulting in spatially distinct immunological responses, as evidenced in several bat species (Banerjee et

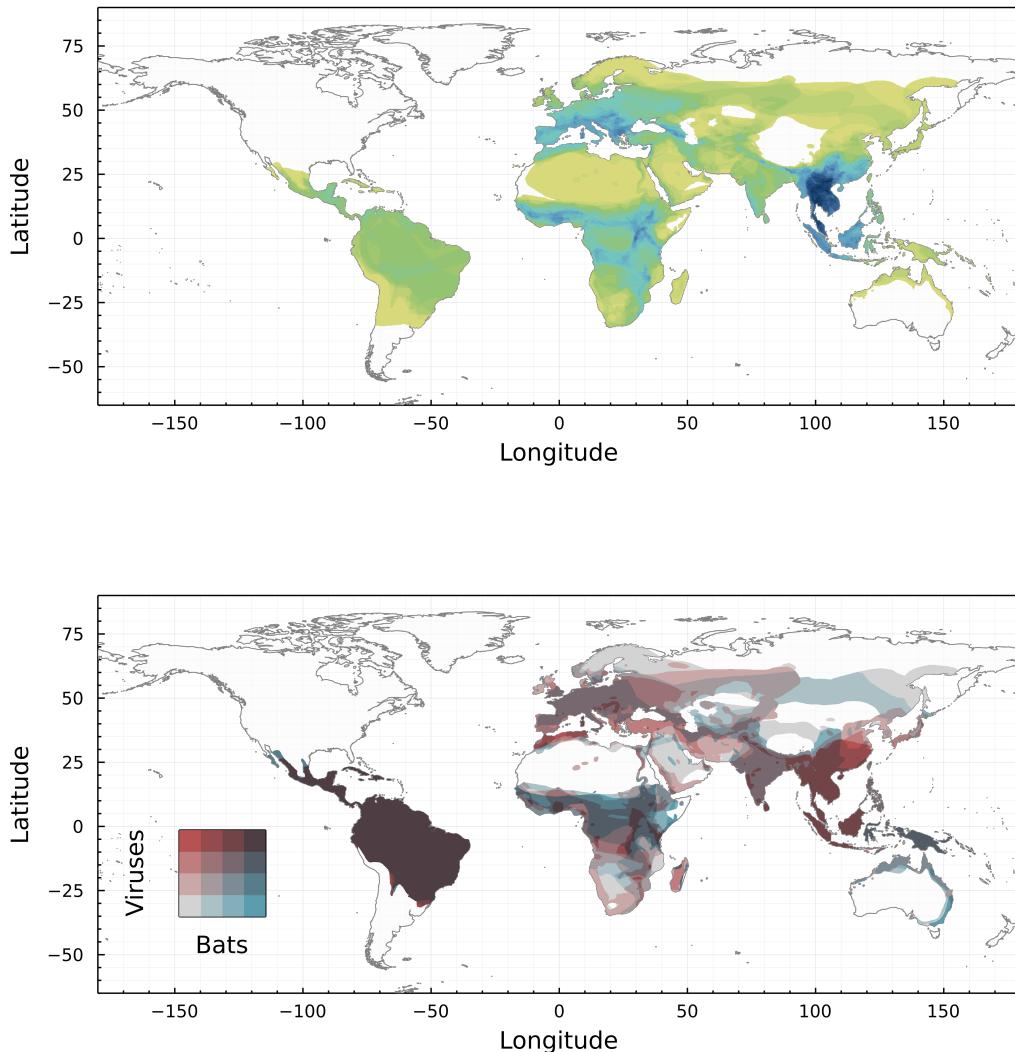


Figure 1 Top panel: relative diversity of known bat hosts of betacoronaviruses. This map shows that the region with the largest number of possible hosts is South-Eastern Asia. Bottom panel: congruence between the evolutionary distinctiveness of the hosts (grey to blue) and the viruses (grey to red). By contrast to the richness map, this reveals that South America has the most evolutionary distinct hosts *and* viruses, whereas South-Eastern Asia has mostly distinct viruses. This is congruent with known results about New World bats being evolutionary distinct, and suggests that they similarly have distinct viruses.

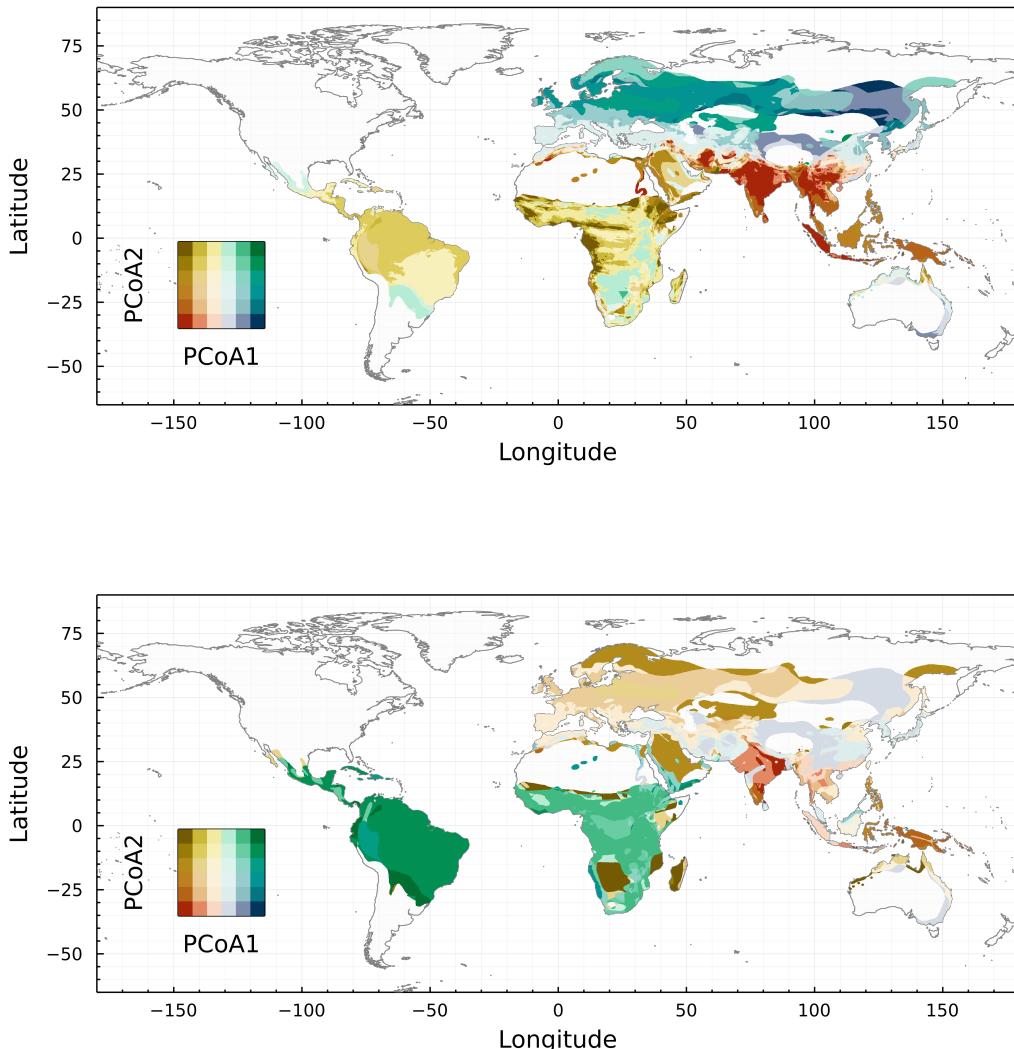


Figure 2 Phylogeographic regions of bats (top) and viruses (bottom) based on the joint analysis of their occurrence and phylogenetic relatedness. The different colors show tendencies to separate alongside the first two components of a PCoA. Note that the PCoA for the bats and viruses are independent, and so cannot be compared directly – that being said, the regions can be compared across maps.

al. 2020). Immune characteristics that allow bats to be better adapted to infection by emerging viruses (Gorbunova et al., 2020; Irving et al., 2021), in addition to being hardcoded in their genome (**Jebb et al. six...**), may be related to a wide variety of diets (Jones et al., 2022; Moreno Santillán et al., 2021; Banerjee et al., 2020; Schneeberger et al., 2013; Muylaert et al., 2021), themselves likely to be driven by spatial effects, especially at the local scale – bats, indeed, occupy a variety of environments, and therefore display a variety of adaptations to these environments.

In fig. 2, we show a projection of the phylogeographic signal of bats (top) and viruses (bottom) in space; the distinct groupings (represented by different colors symbolizing positions in the subspace formed by the first two axes of the PCoA) are essentially equivalent between the two groups, and can be coarsely delineated as southeast Asia, Eurasia above a northing of 25, and Africa and south America. These results suggest that, although the evolutionary distinctiveness of the bat/betacoronavirus complex varies spatially, the system shows an important degree of spatial consistency, with a reduced number of bioregions. Available information describing the spillover of zoonotic betacoronaviruses of bat origin where data was available before and up through the COVID-19 pandemic puts spillover events of SARS-CoV-2 in Wuhan, China; SARS-CoV in XXX based on the presence of closest known viruses circulating in nature, and a nearby location where serological (antibody) evidence has indicated human exposure to SARS-like viruses (Wang et al. 2018 Virologica Sinica); MERS-CoV in XXX based on index cases avail-

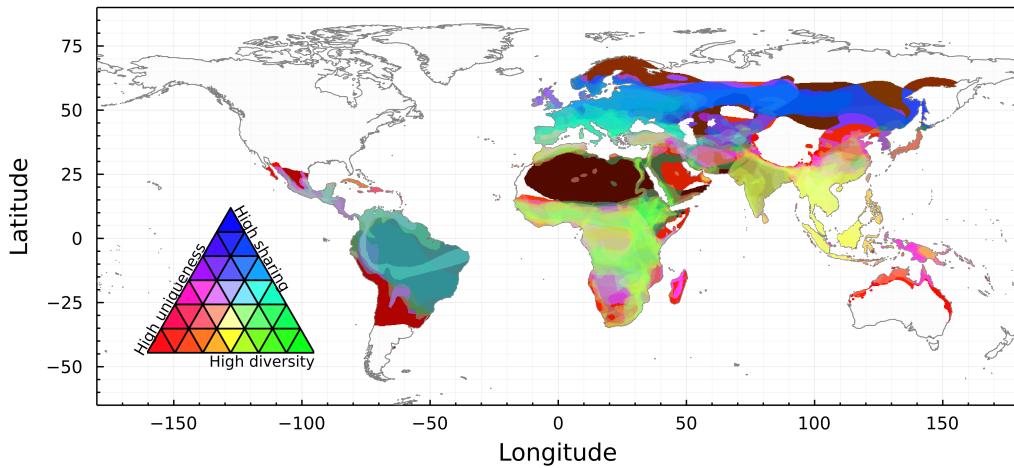


Figure 3 Trivariate additive mapping of the components of risk in the red/green/blue, where high virus sharing is encoded in the blue channel, host phylogenetic diversity in the green channel, and compositional uniqueness in the red channel. A pixel that would maximize all measures would be a pure white (specifically RGB(1.0, 1.0, 1.0)), and a pixel with the lowest possible values would be pure black (specifically RGB(0.0, 0.0, 0.0)). Therefore, lighter values (the sum of the three channels gets closer to 3) indicate higher risk, and the color indicates the proportional distribution of the factors making up the total risk.

able from a recently-published compendium of cases (Ramshaw et al. 2019). For the latest event, most if not all index cases are presumed to be camel-to-human transmission, and the precise origin point (if it exists) of MERS-CoV in bats is uncertain. Recent recombinant canine coronavirus spillover events in Haiti ([ref](#)) and Europe ([ref](#)) are not relevant here, as bats' involvement in these cycles of transmission have been supposed to be non-existent.

2.3. Coevolution-informed spillover risk is different in space As host richness, joint distinctiveness, or phylogeographic structure suggest that the bat/betacoronavirus complex is globally fragmented enough to give rise to both different levels of risk (as evidenced by the spatial location of spillover events) and different types of co-evolutionary dynamics, we turn to the Geographic Mosaic Theory of Coevolution [REF](#) to provide a measure of risk accounting for multiple processes. In fig. 3, we overlapped three components of spillover risk: viral sharing, *i.e.* the chance that two bats will share viruses overall; Local Contribution to Beta Diversity, *i.e.* the fact that a bat community is compositionally unique compared to the average compositional similarity across the entire system; finally, host phylogenetic diversity, *i.e.* how dispersed the bats in a location are within the tree of life. This approach leads to the definition of broad biogeographic regions of risk, where the same color represents the same type of risk. By way of contrast to figures fig. 1 and fig. 2, these regions do not necessarily overlap with previous spatial partitions of the bat/betacoronavirus complex.

From the perspective of spillover risk, the most important combination of factors is a high phylogenetic diversity of hosts with low viral sharing; this, essentially, means that very different betacoronaviruses could co-exist within the same place. This is particularly the case given that betacoronaviruses often evolve and even achieve host shifts through recombination, which requires the co-occurrence of sufficiently distinct viruses to be a major driver of emergence. In fig. 3, this corresponds to yellow to pale green areas, which are essentially limited to South-Eastern Asia, and to some part of Sub-Saharan Africa. Adopting a geographic mosaic theory perspective on risk, other regions of the world are of lesser concern fig. 4. Our risk decomposition does not account for viral diversity or distinctiveness. The simple rationale behind it is that the acquisition of viral data is rarely disconnected from the acquisition of host data; furthermore, there are more sources of information on hosts than on viruses, allowing to develop a host-centric perspective on risk. Areas with high bat diversity and high turnover *may* facilitate the evolutionary radiation of viruses, matching previous findings that the diversification of bat coronaviruses is driven largely by host shifts (inter-genus or higher levels of cross-species transmission) and, to a lesser degree, cospeciation and sharing (intra-genus cross-species transmission; **Anthony et al. 2017**). This diversification is not an actual risk factor for spillover itself, but acts downstream of a spillover event by increasing the random chance of the emergence of a virus with the raw genomic components required for the potential to infect humans.

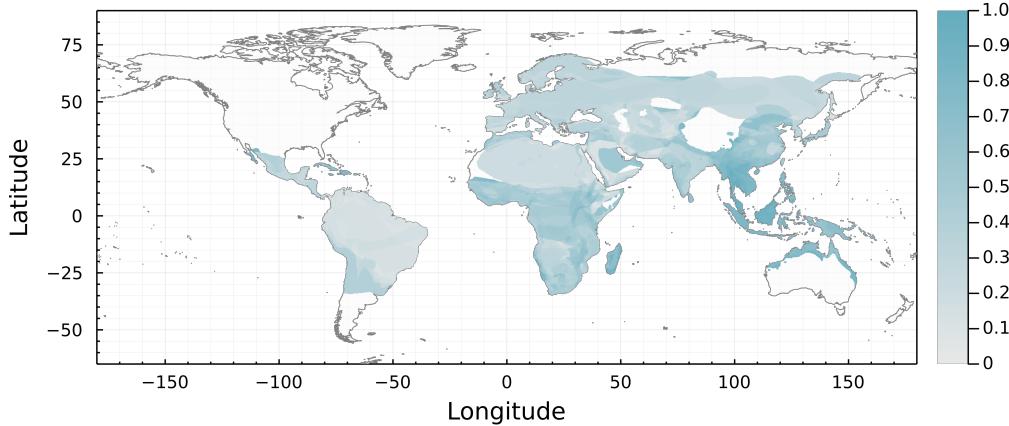


Figure 4 Extraction of a measure of risk based on the colorimetric space from fig. 3. The risk is a composite measure of the color value and angular distance to the yellow hue, as defined in the methods, ranged in the unit space. Based on this analyses, regions at high risk of spillover are southeast Asia and Madagascar.

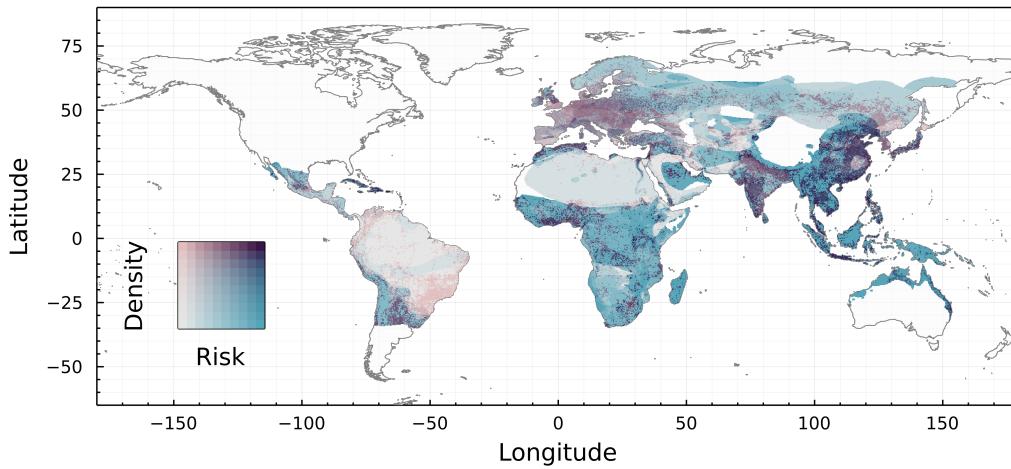


Figure 5 Overlap of the percent of each pixel occupied by urbanized structures, representing the degree of settlement, on the risk map. Darker pixels correspond to more risk, in that the GMTC-derived risk of fig. 4 is high and the pixel is densely occupied by human populations. This approach increases the relative risk of several regions in Africa, and concentrates highlights the risk in India, southeast China, and the arabic peninsula.

2.4. Human occupancy drives different levels of effective risk globally Based on the previous result, we extracted the yellow component of the risk map (TP add methods), to provide a single measure of risk varying between 0 and 1. This measure is presented in fig. 4. However, this maps the potential risk, which must be weighed by the potential for contacts with humans. As a proxy for this measure, we used the proportion of build/urban land from the EarthEnv dataset: this is a reasonable proxy for the density of humans per unit area, which increases the probability of pathogen spread more widely (Hazarie et al., 2021). Since human activity is required to amplify the frequency of virus encounters and thus create areas of viral amplification, mapping the potential risk against measures of land use is required to generate a more actionable assessment of risk. This map is presented in fig. 5. Most of South America and Europe are at low risk, as although densely populated, settlements tend to be in areas with lower potential risk. However, this mapping reveals that South-East Asia, the Indian subcontinent, and parts of sub-Saharan Africa, are at high risk due to the overlap between built areas and bat communities representing more opportunities for cross-species transmission of betacoronaviruses.

Conclusion

Our study focuses largely on the biogeography of hosts. Yet, we know that viruses with high host plasticity, that is, the ability of a given virus to adapt to various taxonomic orders and ecological groups (Kreuder Johnson et al., 2015); are more likely to amplify viral spillover, followed by secondary human-to-human transmission, and geographical spread (Hazarie et al., 2021). High viral host plasticity is an especially important trait for RNA viruses such as betacov (Kreuder Johnson et al., 2015; Haddad et al., 2021). Indeed, our analysis of viral sequences reveals that Latin America is a hotspot of viral distinctiveness, suggesting that this part of the bats-betacov system may be undergoing independent evolutionary dynamics (related species sharing viruses that are different from the rest of the global pool). The other hotspot of viral distinctiveness is S.E. Asia, in which richness is high but sharing is low; this suggests a different type of evolutionary dynamics (unrelated viruses coevolving with evolutionarily distinct hosts, generating high diversity locally). Both of these areas should be priority areas for sampling, especially since (**Becker?**) advance that they harbor undiscovered hosts of beta-coronaviruses. This diversity of hosts, and the mechanisms by which the exchange of viruses occurs between species, is largely affected by the local environmental conditions and environmental change.

There are several factors that drive changes in the diversity of bats (Alves et al., 2018), but human activities' effects on the ecosystem (like modifications of land use) could significantly decrease it. Therefore, it can be suggested that changes in the diversity of betacovs in bats are linked to their biogeographic variation, and human population density and other anthropogenic factors are decisive moderators for its implications in public health. With the increase of contact between humans and potential hosts, we also increase the risk of emergence of novel diseases (Johnson et al., 2020), as previous studies on RNA viruses suggest the importance of host phylogeography at the time of virus dispersal (Gryseels et al., 2017). One of these scenarios where interaction between bats and humans can occur can be seed dispersal in tropical agroecosystems. It opens the discussion of whether the fruits thrown by bats not only disperse seeds but could also be a source of indirect interaction between viruses of bat origin and humans (Deshpande et al., XX). This represents a challenge for conservation strategies and disease ecology since we have areas with both potential for the acquisition of zoonotic viruses and bat-human interaction; in particular, the challenge lies in the fact that actual exposure must be quantified from several scenarios, including both direct and indirect bat - human interaction.

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