

The coevolutionary mosaic of bat-betacoronaviruses spillover risk

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1 Spillover risk is not unidimensional. From the standpoint of an animal community, *i.e.* a pool of suitable
2 hosts, it is driven by a multiplicity of factors (Plowright et al. 2017). The global richness of hosts is one
3 such component commonly mentioned/analysed (see *e.g.* Anthony et al. 2017 for coronaviruses), but
4 there is an argument to be made that species who are not competent (or know) hosts of a specific virus
5 genus may not factor into this (Plowright et al. 2015), or that species who are assumed to share viruses at
6 different rates should be weighted accordingly (Albery et al. 2020). In mammals, key functional traits (for
7 which phylogeny is a reasonable proxy) are determinants of the spillover potential (Olival et al. 2017);
8 these include, notably, body mass and affinity for urban environments (Albery et al. 2022). Finally,
9 especially when the pool of potential hosts spans the entire globe, there may be local host pools that are
10 highly unique; not having been observed in other locations, these can act on the overall risk either by
11 providing novel contact opportunities, reflecting unique host-environment combinations (Engering et al.
12 2013), or facilitating rapid evolutionary changes in specialism of their pathogens (Agosta et al. 2010). In
13 the specific case of generalist pathogens, there is conceptual and empirical support to the idea that these
14 community- level mechanisms are even more important in driving the overall risk (Power and Mitchell
15 2004).

16 Bats are important reservoir hosts for different classes of microorganisms (Chu 2008, Donaldson 2010, Li
17 2010), some of which can threaten human health. Chiropterans emerged around 64 million years ago and
18 are one of the most diverse mammalian orders, with an estimated richness of more than 12000 species,
19 (Peixoto et al. 2018) and 14325 known species (Simmons and Cirranello 2020). They exhibit a broad
20 variety of habitat use, behaviour, and feeding strategies, resulting in their playing an essential role in the
21 delivery of several ecosystem services tied to important ecosystem-derived benefits (Kasso and
22 Balakrishnan 2013). For example, over two-thirds of bats are known to be either obligate or facultative
23 insectivorous mammals, therefore playing an important role in the regulation of insect pests that can
24 affect crops (Williams-Guillén et al. 2008, Voigt and Kingston 2016), and vectors of diseases that put a risk
25 on human health (Gonsalves et al. 2013a, b). Because bats are globally distributed and have a long
26 evolutionary history, phylogeographic and biogeographic approaches are required to shed light on the
27 extant distribution of coevolutionary processes between bats and the pathogens they carry. Not all areas in
28 which bats, viruses, and human are co-occurring are facing a risk of spillover towards human populations,
29 and the areas in which this risk exist may not be facing risks of the same nature and magnitude.

30 In this paper, we examine the biogeographic structure of bats-betacoronaviruses associations, based on a

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

42 **Methods**

43 **Known betacoronavirus hosts**

44 We downloaded the data on bats hosts of betacoronaviruses assembled by Becker et al. (2022) from
45 <https://www.viralemergence.org/betacov> on Aug. 2021, and filtered it to “known” hosts (established
46 before the emergence of SARS-CoV-2) and “novel” hosts (confirmed through sampling since the
47 emergence of SARS-CoV-2). This database was assembled by a combination of data mining and literature
48 surveys.

49 **Bats occurrences**

50 We downloaded the rangemap of every extant bat species that was either classified as an empirically
51 documented or a suspected host of beta-coronaviruses (Becker et al. 2020), according to recent IUCN data
52 (IUCN 2021). The range maps were subsequently rasterized at a resolution of approximately 1 km. For
53 every pixel in the resulting raster where at least one bat host of betacoronavirus was present, we extract the
54 species pool, which was used to calculate the following risk assessment components: phylogenetic
55 diversity, bat compositional uniqueness, and predicted viral sharing risk.

56 **Bats phylogeography**

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

67 **Bats compositional uniqueness**

68 For every species pool, we measured its Local Contribution to Beta-Diversity (Legendre and De Cáceres
69 2013); LCBBD works from a species-data matrix (traditionally noted as Y), where species are rows and sites
70 are columns, and a value of 1 indicates occurrence. We extracted the Y matrix assuming that every pixel
71 represents a unique location, and following best practices (Legendre and Condit 2019) transformed it
72 using Hellinger's distance to account for unequal bat richness at different pixels. The correction of raw
73 community data is particularly important for two reasons: first, it prevents the artifact of richer sites
74 having higher importance; second, it removes the effect of overall species richness, which is already
75 incorporated in the phylogenetic diversity component. High values of LCBBD indicate that the pixel has a
76 community that is on average more dissimilar in species composition than what is expected knowing the
77 entire matrix, i.e. a more unique community.

78 **Viral sharing between hosts**

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

83 **Composite risk map**

84 To visualize the aggregated risk at the global scale, we combine the three individual risk components
85 (phylogenetic diversity, compositional uniqueness, and viral sharing) using an additive color model
86 (Seekell et al. 2018). In this approach, every risk component gets assigned a component in the RGB color
87 model (phylogenetic diversity is green, compositional uniqueness is red, and viral sharing is blue). In
88 order to achieve a valid RGB measure, all components are re-scaled to the [0,1] interval. This additive
89 model conveys both the intensity of the overall risk, but also the nature of the risk as colors diverge
90 towards combinations of values for three risk components.

91 **Viral phylogeography**

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

104 **Viral evolutionary diversification**

105 We first tested the hypothesis that hotspots of viral diversification would track hotspots of bat
106 diversification. To do so, we plotted the number of known bat hosts (specifically only those included in the
107 phylogeny, so there was a 1:1 correspondence between data sources) against the “mean evolutionary
108 distinctiveness” of the associated viruses. To calculate this, we derived the fair proportions evolutionary
109 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.

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 & Jetz (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'; 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.

Outbreaks data geo-referencing

Finally, we provide a summary visualization of what available information describes the spillover of zoonotic betacoronaviruses of bat origin where data was available before and up through the COVID-19 pandemic. The SARS-CoV-2 outbreak was georeferenced to the initial case cluster in Wuhan, China; SARS-CoV was georeferenced based on the cave with the closest known viruses circulating in nature (Hu et al. 2017 PLoS Pathogens), and a nearby location where serological (antibody) evidence has indicated human exposure to SARS-like viruses (Wang et al. 2018 Virologica Sinica). For MERS-CoV, we presented the index cases available from a recently-published compendium of MERS-CoV cases (Ramshaw et al. 2019); these are largely if not all presumed to be camel-to-human transmission, and the precise origin point of MERS-CoV in bats is uncertain. Not shown is a recent case of a recombinant canine coronavirus

137 that showed the ability to infect humans, both because this study was published after the beginning of the
138 COVID-19 pandemic and because bats' involvement in this cycle of transmission has been marginal to
139 non-existent.

140 **Results**

141 **Host distribution**

142 Chiroptera are an hyperdiverse group, distributed in a large part of the world, and are an important
143 reservoir for different strains of betacoronaviruses (Drexler et al., 2014); this has attracted attention to
144 areas where high diversity of bats can be an important issue for human health (Calisher et al., 2006).
145 Accordingly, we collected the IUCN rangemaps for known hosts of betacoronaviruses, to illustrate where
146 hotspots of host diversity are. These results are presented in Fig xx.a. As per our current knowledge of
147 which bats are hosts of betacoronaviruses, these hotspots are primarily South-East Asia, parts of Europe,
148 and to a lesser extent sub-saharan Africa. Even the subset of chiroptera that are hosts of betacoronaviruses
149 fits the evolutionary timeline of the group. Chiropterans can be classified as Microchiroptera and
150 macrochiroptera, where macrochiroptera have an older history from an evolutionary perspective
151 compared to microchiroptera (Springer, 2013; Teeling et al., 2005). South-East Asia has a high diversity of
152 bats (Kingston, 2010), and our results show that part of that diversity includes betacoronavirus hosts. High
153 density of hosts sharing the same virus (albeit possibly different strains) calls into question the evolution
154 of the bat antiviral immune system and its co-evolution with viruses, which may result in distinct
155 immunological responses in different areas, as evidenced in other bat species (Banerjee et al., 2020)

156 **Viral evolutionary distinctiveness**

157 Higher host diversity may not result in a higher viral diversity; for this reason, we quantified and mapped
158 the evolutionary distinctiveness of betacoronaviruses, based on Viral evolutionary distinctiveness
159 largely tracks host diversity, particularly in southern China but oddly not throughout the rest of southeast
160 Asia, perhaps indicating that many distinctive viruses remain to be discovered in this region (an idea that
161 is unsurprising given the growing realization, around the emergence of SARS-CoV-2, that a unique
162 lineage of similar viruses are widespread in bats but still mostly undescribed). The most distinct

betacoronaviruses are found in South America, a region with a comparatively lower number of hosts; this suggests that the South American bat-betacoronavirus complex has been more isolated, and is probably undergoing 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), and adding more viruses would bring the distinctiveness of known sequences down. Previous work has suggested the Americas may be a hotspot of both undiscovered bat viruses in general (Olival) and coronavirus specifically (Anthony), though not necessarily betacoronaviruses, and particularly not those in clades with notable zoonotic potential (c.f. Anthony).

Geographic Mosaic of bat-betacoronavirus risk

In order to turn the hypotheses based on the Geographic Mosaic Theory of Coevolution into a measure of risk, we overlapped three components: 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, the phylogenetic diversity, i.e. how dispersed the bats in a location are within the tree of life. These results are presented using an additive color mapping in Figure xx, and lead to the definition of broad biogeographic regions of risk, where the same color represents the same type of risk. Pairwise maps of the three components are present in supplementary materials.

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 betacoronavirus 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. xx, 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.

Available data on bat betacoronavirus spillover into humans (TP overlay on the figure) is limited and circumstantial at best for these purposes, but our risk maps suggest that the areas predicted by prior expectations about host biogeography correspond loosely to those where previous emergence events have been recorded. Areas with high bat diversity and high turnover may facilitate the evolutionary radiation of

191 viruses, matching previous findings that the diversification of bat coronaviruses is driven largely by host
192 shifts (inter-genus or higher levels of cross-species transmission) and, to a lesser degree, cospeciation and
193 sharing (intra-genus cross-species transmission; Anthony et al. 2017). This diversification - while not an
194 actual risk factor for spillover itself - likely increases the random chance of a virus with the raw genomic
195 components required for the potential to infect humans.

196 **Global distribution of spillover risk**

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

209 **Discussion**

210 Driven by the need to understand the ecological factors involved in the emergence of viral pathogens, we
211 spatially mapped bat-betacoronavirus interactions worldwide, using (i) a database of known betacov
212 hosts(Becker et al., 2020), and (ii) range maps for the hosts according to IUCN (IUCN 2021). To reflect the
213 fact that the risk posed by viruses has many ecological origins, we quantified the phylogenetic diversity of
214 hosts, their compositional uniqueness, and the expected viral sharing. Because these components of risk
215 matter when contrasted to human density, we compared them to a proxy, namely the proportion of each
216 pixel that is covered by urban or built land. This provides a synthetic risk map, allowing to identifying of
217 hotspots where the bat-betacoronavirus system may originate viruses in humans. SE Asia is one of the

218 regions with the highest risk since, according to our results, several of its conditions could increase the
219 risk of transmission of the virus.

220 Bats are found worldwide and are one of the most diverse groups among mammals (Moratelli & Calisher,
221 2015). Previous research (Anthony et al., 2017; Mollentze & Streicker, 2020) states that locally diverse bat
222 communities could maintain more viruses and hence, a higher probability of having a pathogen that could
223 represent a risk for human health. This probability involves multiple factors, among which the relatedness
224 of hosts (which can make the jumps easier (Longdon et al., 2011; Mollentze et al., 2020; Wolfe et al., 2007),
225 and the overall tendency of hosts within a locality to share viruses, which may limit viral diversity because
226 of within-host competition (Leeks et al., 2018; Sallinen et al., 2020). Species richness, therefore, is not a
227 sufficient measure of viral risk. This is exemplified in our results, where both South America and
228 South-Eastern Asia have a high species richness of betacov hosts, but only the latter region has a high risk.
229 Specifically, because previous studies propose that Asia is important when it comes to understanding the
230 evolutionary origin of various mammalian taxa (Beard C K, 1988). Including bats (Yu et al., 2014), which
231 could support the relationship between evolutionary time and the development of an immune system
232 with characteristics that allow them to be better adapted to infection by emerging viruses (Gorbunova et
233 al., 2020; Irving et al., 2021) may be related to a wide variety of diets (Jones et al., 2022; Moreno Santillán
234 et al., 2021; Banerjee et al., 2020; Schneeberger et al., 2013).

235 Our study focuses largely on the biogeography of hosts. Yet, we know that viruses with high host
236 plasticity, that is, the ability of a given virus to adapt to various taxonomic orders and ecological groups
237 (Kreuder Johnson et al., 2015); are more likely to amplify viral spillover, followed by secondary
238 human-to-human transmission, and geographical spread (Hazarie et al., 2021). High viral host plasticity is
239 an especially important trait for RNA viruses such as betacov (Kreuder Johnson et al., 2015; Haddad et al.,
240 2021). Indeed, our analysis of viral sequences reveals that Latin America is a hotspot of viral
241 distinctiveness, suggesting that this part of the bats-betacov system may be undergoing independent
242 evolutionary dynamics (related species sharing viruses that are different from the rest of the global pool).
243 The other hotspot of viral distinctiveness is S.E. Asia, in which richness is high but sharing is low; this
244 suggests a different type of evolutionary dynamics (unrelated viruses coevolving with evolutionarily
245 distinct hosts, generating high diversity locally).

246 This diversity of hosts and how the exchange of viruses occurs between species, is largely affected by the
247 different environmental changes, as the case of sarbecovirus bats reservoirs (Muyllaert et al., 2021) where

they are affected by the area of the cave or the alteration of the forest, which could result in modifications of host distribution. Additionally, our results highlight the importance of Asia as a betacov hotspot, which is consistent with recent studies (Muylaert et al., 2021), where projections on this area suggest that new future events of sarbecovirus viral exchange might be easily spread among species or humans.

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., 2022). This represents a challenge for conservation strategies and disease ecology since we have areas with potential zoonotic viruses and bat-human interaction. However, it must still be taken into account the quantification of real exposure from several scenarios, where there can be directly or indirectly bat - human interaction.

Comparing scenarios of high viral exchange vs low viral exchange, open the discussion to consider if the best scenario is where viruses easily adapted to multiple hosts but with low virulence or easily ignored by the immune system of the host, or where we have viruses specialized to a specific host, but highly virulent when invade a new host. Accordingly, the understanding of viral-host interactions from a taxonomic and phylogenetic contributes to improving zoonoses surveillance programs.

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