

# The coevolutionary mosaic of bat betacoronavirus emergence risk

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Driven by the need to understand the ecological factors involved in the emergence of *Betacoronavirus* (the genus causing SARS, MERS, and COVID-19 in human) 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 spillover risk posed by betacoronaviruses, reflecting the fact that this risk is best understood through the multi-faceted prism of ecological and evolutionary mechanisms. Our framework reveals that host richness alone, although a component of viral hazard, is not a sufficiently integrative predictor of risk. We offer alternative insights based on viral sharing, host compositional uniqueness, and host phylogenetic diversity and phylogeographic regions. 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 interaction network may facilitate the emergence of novel viruses and their spillover into human populations.

1 Disease emergence is complex, and is driven not only by animal-human contact, but also by the  
2 underlying evolutionary dynamics in viral reservoirs.<sup>1</sup> Although host richness is often used as a superficial  
3 proxy for spillover risk,<sup>2,3</sup> these approaches oversimplify the relevant interspecific heterogeneity in  
4 immunology, behavior, and other traits, and therefore overlook unique host pools that allow for the rapid  
5 evolution of highly divergent viruses.<sup>4</sup> In the case of generalist pathogens like betacoronaviruses, there is  
6 conceptual and empirical support to the idea that these community-level mechanisms are even more  
7 important,<sup>5</sup> particularly given that cross-species transmission may, as a rule, structure viral evolution  
8 more than co-divergence with hosts.<sup>6</sup> This creates a disconnect between coevolutionary theory and most  
9 existing ecological frameworks for mapping spillover risk.

10 The geographic mosaic theory of coevolution (GMTC) attempts to explicitly connect microevolutionary  
11 dynamics to the macroecology and biogeography of symbiotic interactions.<sup>7</sup> The GMTC posits that  
12 coevolutionary processes among pairs<sup>8</sup> or complexes<sup>9</sup> of species are structured in space by the rippling  
13 effects of abiotic conditions onto evolutionary mechanisms, giving rise to fragmented systems with  
14 different ecologies over large spatial extents.<sup>10</sup> The GMTC predicts a spatial fragmentation of  
15 coevolutionary dynamics under the joint action of three processes:<sup>11</sup> coevolutionary hot- and coldspots,  
16 which appear when the intensity of *interaction* (in terms of reciprocal fitness consequences) varies  
17 spatially; selection mosaics, wherein the intensity of *selection* varies across space, driven by both the biotic  
18 complexity of the community (locally diverse hosts and viruses are more biotically complex) and the local  
19 favorability of the environment;<sup>12</sup> and trait remixing, which occurs when coevolutionary dynamics change  
20 when community-level *functional traits* change through meta-community dynamics.

21 Here, we apply the GMTC to explore and explain the global biogeography of betacoronaviruses, the group  
22 that includes SARS-CoV, MERS-CoV, and SARS-CoV-2. In their bat reservoirs, coronaviruses evolve  
23 through a mix of host jumps, recombination among disparate lineages, and, to a lesser degree,  
24 co-divergence with their hosts—<sup>2</sup>a mix of mechanisms that creates a complex and nonlinear relationship  
25 between host diversity and viral emergence. Working from a recently published database of bat hosts of  
26 betacoronaviruses, we test whether spatial structure in bat-betacoronavirus coevolution is identifiable at a  
27 global scale. Aiming to explain these patterns, we develop a generalized framework for applying the  
28 GMTC to host-virus interactions, with a specific emphasis on the potential to create independent  
29 coevolutionary dynamics (and therefore spatial fragmentation in risk) through heterogeneity. We develop  
30 a trivariate risk assessment system that connects each GMTC mechanism to a quantifiable aspect of

31 host-virus interactions: (i) viral sharing rates in host communities, representing the strength of potential  
32 interaction between viruses and any one host (i.e., places where viruses undergo constant host switching  
33 may be coevolutionary coldspots); (ii) the phylogenetic diversity of hosts, as a proxy for variation in the  
34 immunological mechanisms that antagonize viruses (i.e., the selection mosaic); and (iii) the local  
35 uniqueness of the bat community, representing the potential for viruses to be exposed to novel host traits  
36 (e.g., variation in receptor sequences). Together, we argue that these can be used to identify and map the  
37 evolutionary drivers that—in conjunction with transmission processes (e.g., viral prevalence in reservoirs  
38 and animal-human contact rates)—determine disease emergence risk.

## 39 Results and Discussion

### 40 Bat and betacoronavirus biogeography are broadly consistent

41 Most previous work has assumed that the presence or richness of key groups of bat hosts are predictive of  
42 coronavirus diversity.<sup>2,3</sup> Projecting bat and betacoronavirus phylogeny over space (fig. 1), we find support  
43 for the idea that bat community assembly is directly responsible for a global mosaic of viral evolution. The  
44 distinct groupings (represented by different colors, symbolizing positions in a subspace formed by the first  
45 two phylogenetic principal components) are essentially equivalent between the two groups, and can be  
46 coarsely delineated as (1) south and southeast Asia; (2) east Asia (including northern China), west Asia,  
47 and the Mediterranean coast; (3) Eurasia above a northing of 40; and (4) Africa and Latin America. In  
48 some cases, this diverges from expectations about coronavirus biogeography: for example, previous work  
49 has rarely flagged India as a region of interest, but for both bats and betacoronaviruses, the subcontinent  
50 falls into the same regions as the southeast Asian peninsula (and indeed, the region is home to known bat  
51 hosts of multiple betacoronavirus subgenera, including nobecoviruses, sarbecoviruses, and  
52 merbecoviruses).<sup>3</sup>

53 [Figure 1 about here.]

54 Overall, these results suggest that the boundaries of bat and betacoronavirus biogeographic regions are  
55 largely consistent. This may be surprising, given that cross-species transmission may play a stronger role  
56 in coronavirus diversification than cospeciation—<sup>2</sup>a property that would theoretically allow for

57 substantial broad divergence in their biogeography. However, host jumps at the family level or higher are  
58 relatively rare and significant events in coronavirus evolutionary history;<sup>2,13</sup> as a result, the mosaic of  
59 betacoronavirus phylogeography is assembled from a set of overlapping smaller coevolutionary systems,  
60 superimposed in space and filtered by the importance of different subgroups in local host communities.  
61 For example, the most speciose and cosmopolitan family of bats, the vesper bats (Vespertilionidae), are  
62 considered the primary hosts of the subgenus *Merbecovirus* (MERS-like viruses);<sup>3,13</sup> but in the Americas,  
63 where merbecoviruses are the only lineage present, they have only been found in other bat taxa (e.g.,  
64 Molossidae, Phyllostomidae).<sup>14–17</sup> At the coarsest scale, these heterogeneities are lost, and betacoronavirus  
65 biogeography tracks the deep rifts in bat evolutionary history—but within broad regions, the component  
66 coevolutionary systems may have very different dynamics.

## 67 **Hotspots of bat and betacoronavirus biodiversity are distinct**

68 Bats, the second most diverse groups of mammals, are found worldwide; gradients in their species  
69 richness generally track broader patterns of mammal diversity, with a striking Neotropical hotspot  
70 (especially in the Amazon basin) and a secondary hotspot centered in the southeast Asian peninsula.  
71 These hotspots of bat diversity are generally presumed to be hotspots of viral adaptive radiation, and  
72 therefore areas of concern for human health.<sup>2,18</sup> However, the hotspots of known bat betacoronavirus  
73 hosts show a distinct pattern, with primary hotspots (both in terms of size and higher values) of host  
74 richness situated in southeast Asia, parts of southern Europe, and to a lesser extent parts of Africa in the  
75 -25-0 range of latitudes (fig. 2; top). Although hundreds of species likely host undiscovered  
76 betacoronaviruses, machine learning predictions have suggested that these undiscovered reservoirs should  
77 follow the same diversity gradient.<sup>19</sup> In principle, these hotspots of locally-diverse, virus-rich bat  
78 communities should drive more adaptive diversification in their viruses.

79 [Figure 2 about here.]

80 However, we find that the global pattern of betacoronavirus phylogenetic distinctiveness is quite distinct  
81 from both bat host richness and phylogenetic distinctiveness (fig. 2; bottom). In contrast to the sparsity of  
82 Neotropical betacoronavirus hosts, South and Central America have the most evolutionary distinct hosts  
83 and viruses, followed by secondary hotspots in southeast Asia and the Rift Valley region have mostly  
84 distinct viruses. Some degree of sampling bias may contribute to these patterns: for example, the

85 Neotropics are one of the places where the fewest bat betacoronavirus sequences have been generated  
86 (cite2), resulting in a sparser phylogenetic tree, and artificially inflating distinctiveness; conversely,  
87 disproportionate research effort in eastern China<sup>20</sup> may have led to a more complete inventory of the local  
88 diversity of coronaviruses, again inflating these metrics relative to underlying patterns. Even accounting  
89 for these potential biases, though, there is obvious heterogeneity in betacoronavirus evolutionary  
90 distinctiveness that is distinct from overall bat diversity.

91 Overall, these patterns recapitulate the evolutionary history of both the order Chiroptera and the genus  
92 *Betacoronavirus*. Horseshoe bats (Rhinolophidae) include the reservoirs of the SARS-like viruses  
93 (subgenus *Sarbecovirus*), the group of pandemic threats that have been of the greatest interest to  
94 researchers<sup>13</sup> (and so have been sampled most intensively).<sup>20</sup> The hotspots of host richness and viral  
95 diversity in southeast Asia—both of which are disproportionately high, considering the global landscape  
96 of bat species richness—are almost entirely driven by viral adaptive radiation through host switching  
97 within this clade<sup>3,19</sup>. In contrast, the Neotropical hotspot of viral distinctiveness is driven by isolation by  
98 host vicariance. Out of the four main groups of betacoronaviruses, only merbecoviruses have been found  
99 in animals in the Americas—an introduction that is generally presumed to be ancient.<sup>3,21</sup> While  
100 comparatively understudied, New World merbecoviruses have been found in the ghost-faced bats  
101 (Mormoopidae), Neotropical leaf-nosed bats (Phyllostomidae), and free-tailed bats (Molossidae).<sup>14–17</sup> The  
102 former two groups and a clade of the latter are endemic to the Neotropics, while the explosive adaptive  
103 radiations of the phyllostomids are responsible for the hotspot of bat diversity in the Amazon.<sup>22</sup> Together,  
104 these clades of New World bats play host to a distinct regime of betacoronavirus coevolution.

## 105 Coevolutionary regimes structure evolutionary risk of zoonotic emergence

106 The existence of well-defined cophylogenetic regions suggests that the bat-betacoronavirus system is  
107 spatially fragmented enough to create differential coevolutionary processes; in turn, the coevolutionary  
108 mosaic contributes to heterogeneity in emergence risk. These ideas are, respectively, supported by the  
109 existence of hotspots of viral uniqueness and the diverse origins of human betacoronaviruses. Together,  
110 these ideas point to a predictable relationship between host community structure and coevolutionary  
111 pressure: phylogeographic structure in bat hosts—and their diverse immune strategies—<sup>23</sup>creates a  
112 landscape of selective pressure; the trajectory of viruses' coevolutionary response is, in turn, constrained  
113 by the opportunities they have for either coevolutionary specialization or diversification through host

114 jumps and recombination.

115 Based on the geographic mosaic theory of coevolution, we developed a trivariate map of three facets of  
116 coevolutionary pressure (see Methods): (1) *host phylogenetic diversity*: a high diversity of evolutionary  
117 histories should expose viruses to more variation in host immune traits; (2) *host community uniqueness*:  
118 exposure to greater host trait heterogeneity can drive viral diversification, and coevolving with more  
119 unique host communities should create more unique branches of viral evolution; and (3) propensity for  
120 *viral sharing*: frequent cross-species transmission may act as a buffer on selective pressure, while lower  
121 rates of exchange may enable more simultaneous trajectories of viral specialization to coexist within a  
122 given community. We combine global maps of all three to generate a map of coevolutionary regimes,  
123 where close colors represent similar risks, and paler pixels represent overall higher risk (fig. 3). We find  
124 that these regions do not neatly overlap with those defined in fig. 1 or fig. 2, reinforcing the notion that  
125 local-scale coevolutionary mosaics can form within cophylogenetic regions.

126 [Figure 3 about here.]

127 The greatest evolutionary potential for zoonotic emergence exists where pathogen pools have a high  
128 genetic diversity and high propensity for cross-species transmission. In our framework, emergence risk is  
129 therefore maximized under higher phylogenetic diversity (viruses are exposed to different host clades),  
130 higher host uniqueness (viruses are experiencing novel, heterogeneous host traits combinations), and low  
131 to medium viral sharing (host-virus pairs can coevolve independently, but divergent viruses may still have  
132 opportunities for recombination). In fig. 3, this corresponds to yellow areas (dynamics dominated by low  
133 viral sharing, with equal contributions of selection mosaics and trait remixing; southeast Asia, and the  
134 Indian sub-continent), green-yellow areas (dynamics with low viral sharing but dominated by the  
135 selection mosaic effect of host diversity; sub-Saharan Africa), and red-yellow areas (dynamics with low  
136 viral sharing but dominated by trait remixing in host communities; the Middle East). Translating this axis  
137 of variation back into a univariate risk map (fig. 4) highlights that this evolutionary landscape has a  
138 striking correspondence to regions where zoonotic betacoronaviruses have previously emerged.

139 Compared to approaches that map emergence risk based only on the number of known bat hosts of  
140 betacoronaviruses, our framework suggests regions where high viral sharing dominates coevolutionary  
141 dynamics—such as Latin America, or Eurasia above a northing of 30—would pose less of a relative risk of  
142 zoonotic emergence. Nevertheless, areas of high host uniqueness coupled with high viral sharing

143 (red-to-pink in fig. 3) could create hotspots facilitated by viral codivergence. Our framework identifies  
144 Madagascar, where most bat species are endemic following evolutionary divergence from sister species in  
145 both African and Asian continents,<sup>24</sup> as one such hotspot; interestingly, a recent study<sup>25</sup> reported a novel  
146 and highly divergent lineage of nobecoviruses from Madagascar-endemic pteropid bat species (*Pteropus*  
147 *rufus* and *Rousettus madagascariensis*), again supporting the predictive power of the coevolutionary  
148 framework.

149 [Figure 4 about here.]

## 150 Human landscapes filter the geography of emergence risk

151 The relationship between the underlying pathogen pool and emergence risk is mediated by both  
152 human-wildlife interfaces (the probability of spillover) and opportunities for onward transmission (the  
153 probability that spillovers become epidemics)<sup>1</sup>. As a proxy for both, we finally overlaid the risk component  
154 from the composite map (see above) with the proportion of built land, as a proxy for a mix of habitat  
155 disturbance, potential for bat synanthropy or contact with bridge hosts like livestock,<sup>26,27</sup> and human  
156 population density and connectivity<sup>1,28,29</sup> (fig. 5). Accounting for these factors, most of South America and  
157 Europe are at comparatively lower risk, as—although densely populated—settlements tend to be in areas  
158 with lower potential risk. Conversely, regions like Malaysia and the northern coast of Australia have a  
159 high evolutionary risk component, but should represent a relatively lower effective risk due to low human  
160 density. However, southeast Asia, the Indian subcontinent, and scattered hotspots in sub-Saharan Africa  
161 are at high risk due to the overlap between human populations and natural opportunities for cross-species  
162 transmission of betacoronaviruses.

163 [Figure 5 about here.]

164 Reassuringly, these predictions correspond to the geographic origins of the three bat-origin coronaviruses  
165 that have recently emerged in human populations. While available information puts the spillover of  
166 SARS-CoV-2 in a live animal market in Wuhan, China, the ultimate origin of the virus is almost certainly  
167 in a divergent lineage of sarbecoviruses from the Indochinese peninsula that was poorly characterized  
168 prior to the pandemic.<sup>30–32</sup> Similarly, the SARS-CoV outbreak began in Guangdong province in 2002,  
169 reaching humans through small carnivore bridge hosts, but was eventually traced back to a set of likely

170 progenitor viruses found in cave-dwelling horseshoe bats in Yunnan province;<sup>33</sup> nearby, antibody  
171 evidence has indicated human exposure to SARS-like viruses.<sup>34</sup> MERS-CoV was originally detected in  
172 Saudi Arabia, accompanied by a nearly identical virus sequenced from an Egyptian tomb bat (*Taphozous*  
173 *perforatus*),<sup>35</sup> but is widespread in camels in East Africa and the Middle East, and may have reached its  
174 bridge host decades earlier than originally supposed;<sup>36</sup> as a result, the geography of the original  
175 bat-to-camel transmission is still widely regarded as uncertain. All of these are broadly consistent with the  
176 risk factors we identify. Notably, India and west Africa are additional hotspots that have yet to experience  
177 the emergence of a bat coronavirus into human populations, but may still be at risk—particularly given  
178 known gaps in bat surveillance,<sup>20</sup> and a dense population in both regions with global connectivity. In any  
179 of these regions, surveillance on viral reservoirs can be paired with targeted monitoring of high-risk  
180 human populations (i.e., those with regular wildlife contact)<sup>37</sup> for maximum impact.

## 181 Conclusion

182 Bats are important reservoir hosts for different classes of microorganisms, many of which a threat to  
183 human health.<sup>38,39</sup> Chiropterans emerged around 64 million years ago and are one of the most diverse  
184 mammalian orders, with an estimated richness of more than 1400 species.<sup>40,41</sup> They exhibit a broad variety  
185 of habitat use, behaviour, and feeding strategies, putting them at key positions in the delivery and  
186 provisioning of several ecosystem services, tied to important ecosystem-derived benefits to human.<sup>42</sup> For  
187 example, bats are an essential component of many seed-dispersal networks.<sup>43</sup> Over two-thirds of bats are  
188 known to be either obligate or facultative insectivores, therefore actively contributing for agricultural pest  
189 control,<sup>44,45</sup> and vectors of pathogens that put a risk on human health.<sup>46,47</sup> Because bats are globally  
190 distributed and have a long evolutionary history, phylogeographic and biogeographic approaches are  
191 required to shed light on the contemporary distribution of coevolutionary processes between bats and the  
192 pathogens they host. Not all areas in which bats, viruses, and human are co-occurring are facing a risk of  
193 spillover towards human populations, and the areas in which this risk exist may not be facing risks of the  
194 same nature and magnitude.

195 Here, we propose a simple framework with broad explanatory power that helps contextualize discoveries  
196 like highly divergent nobecoviruses in Madagascar and the previously-neglected adaptive radiation of  
197 sarbecoviruses outside of southern China and throughout southeast Asia. In doing so, it advances

198 ecological theory beyond the current state of the art for global maps of emergence risk. For example,  
199 previous studies that have used host richness as proxy have predicted a high diversity of unsampled bat  
200 viruses,<sup>18</sup> bat coronaviruses,<sup>2</sup> and even specifically betacoronaviruses<sup>19</sup> in both the Amazon and southeast  
201 Asia. While we find that both regions are characterized by highly divergent host and viral communities,  
202 our framework identifies key differences between the regions. We find that Latin America is a hotspot of  
203 both host and viral distinctiveness, suggesting that this branch of the bat-betacoronavirus complex may be  
204 undergoing independent evolutionary dynamics from the rest of the global pool, but with limited potential  
205 for viral diversification—a finding that is supported by previous work indicating a higher rate of  
206 codivergence in Latin America.<sup>2</sup> In contrast, in southeast Asia, host richness and viral distinctiveness are  
207 high but sharing is low; this suggests a different type of evolutionary dynamics that could generate high  
208 local diversity of viruses through host switching and viral recombination (see e.g.,<sup>13</sup> as well as the  
209 discovery of recombinant viruses that share genetic material from both the SARS-CoV and SARS-CoV-2  
210 branches of the Sarbecovirus lineage).<sup>48</sup> Both of these regions are priority areas for sampling, especially  
211 given predictions that they contain many bat hosts of undiscovered betacoronaviruses.<sup>19,20</sup> However, both  
212 the evolutionary and ecological aspects of emergence risk are likely higher in southeast Asia—a fact that  
213 will only become more relevant, as bats track shifting climates and exchange viruses with other species,  
214 creating a hotspot of cross-species transmission unique to the region.<sup>49</sup>

215 The diversity and diversification potential of bats responds to anthropogenic factors others than shifting  
216 climates.<sup>50</sup> Land use changes could significantly decrease bat suitability, notably through effects on diet  
217 and availability of habitats.<sup>51</sup> As our results establish that the diversification of bats betacoronaviruses  
218 happens on top of processes affecting hosts, biogeographic variation in human population density and  
219 anthropogenic disturbances may feed into co-evolutionary dynamics. Increase in humans-hosts contacts  
220 also increase the risk of emergence of novel diseases,<sup>52</sup> so does the changes in landscape connectivity at  
221 local/regional scales.<sup>53</sup> This represents a challenge for both conservation strategies and disease ecology:  
222 some areas can a high emergence risk and more potential for the acquisition of zoonotic viruses through  
223 bat-human encounters.<sup>54</sup> In particular, the challenge ahead lies in the need to quantify actual exposure  
224 (and risk) accounting for several transmission scenarios, including both direct and indirect bat - human  
225 interactions, and feeding back into the provision of ecosystem services by bats.

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236 **Methods**

237 **Known *Betacoronavirus* hosts**

238 We downloaded the data on bats hosts of *Betacoronavirus* from  
239 <https://www.viralemergence.org/betacov> on Apr. 2022,<sup>19</sup> and filtered it to “known” hosts (established  
240 before the emergence of SARS-CoV-2) and “novel” hosts (confirmed through sampling and competence  
241 assays since the initial data collection). The original database was assembled by a combination of data  
242 mining and literature surveys, including automated alerts on the “bats” and “coronavirus” keywords to  
243 identify novel empirical evidence of bats-betacoronaviruses associations; this yielded a total of 126 known  
244 hosts, 47 of which were novel hosts.

245 **Bat occurrences**

246 We downloaded the rangemap of every current bat species that was classified as an empirically  
247 documented host of *Betacoronavirus* from the previous step, according to recent IUCN data.<sup>55</sup> The range  
248 maps were subsequently rasterized using the rasterize function from GDAL<sup>56</sup> at a resolution of  
249 approximately 100kmx100km. For every pixel in the resulting raster where at least one bat host of  
250 *Betacoronavirus* was present, we extract the species pool (list of all known bat hosts), which was used to  
251 calculate the following risk assessment components: bat phylogenetic diversity, bat compositional  
252 uniqueness, and predicted viral sharing risk.

253 **Bat phylogenetic diversity**

254 For every pixel, we measured Faith’s Phylogenetic Diversity<sup>57</sup> based on a recent synthetic tree with robust  
255 time calibration, covering about 6000 mammalian species.<sup>58</sup> Faith’s PD measures the sum of unique  
256 branches from an arbitrary root to a set of tips, and comparatively larger values indicate a more  
257 phylogenetic diverse species pool. We measured phylogenetic diversity starting from the root of the entire  
258 tree (and not from Chiroptera); this bears no consequences on the resulting values, since all branches  
259 leading up to Chiroptera are only counted one per species pool, and (as we explain when describing the  
260 assembly of the composite risk map), all individual risk components are ranged in [0,1]. This measure  
261 incorporates a richness component, which we chose not to correct for; the interpretation of the

262 phylogenetic diversity is therefore a weighted species richness, that accounts for phylogenetic  
263 over/under-dispersal in some places.

## 264 **Bat compositional uniqueness**

265 For every species pool, we measured its Local Contribution to Beta-Diversity;<sup>59</sup> LCBD works from a  
266 species-data matrix (traditionally noted as  $\mathbf{Y}$ ), where species are rows and sites are columns, and a value of  
267 1 indicates occurrence. We extracted the  $\mathbf{Y}$  matrix assuming that every pixel represents a unique location,  
268 and following best practices<sup>60</sup> transformed it using Hellinger's distance to account for unequal bat  
269 richness at different pixels. The correction of raw community data is particularly important for two  
270 reasons: first, it prevents the artifact of richer sites having higher importance; second, it removes the effect  
271 of overall species richness, which is already incorporated in the phylogenetic diversity component. High  
272 values of LCBD indicate that the pixel has a community that is on average more dissimilar in species  
273 composition than what is expected knowing the entire matrix, i.e. a more unique community. Recent  
274 results by<sup>61</sup> shows that LCBD measures are robust with regards to spatial scale, and are therefore  
275 applicable at the global scale.

## 276 **Viral sharing between hosts**

277 For all bat hosts of *Betacoronavirus*, we extracted their predicted viral sharing network, generated from a  
278 previously published generalized additive mixed model of virus sharing by a tensor function of  
279 phylogenetic distance and geographic range overlap across mammals.<sup>62</sup> This network stores pairwise  
280 values of viral community similarity. To project viral sharing values into a single value for every pixel, we  
281 averaged the pairwise scores. High values of the average sharing propensity means that this specific extant  
282 bat assemblage is likely to be proficient at exchanging viruses.

## 283 **Composite risk map**

284 To visualize the aggregated risk at the global scale, we combine the three individual risk components  
285 (phylogenetic diversity, compositional uniqueness, and viral sharing) using an additive color model.<sup>63</sup> In  
286 this approach, every risk component gets assigned a component in the RGB color model (phylogenetic  
287 diversity is green, compositional uniqueness is red, and viral sharing is blue). In order to achieve a valid

288 RGB measure, all components are re-scaled to the [0,1] interval, so that a pixel with no sharing, no  
289 phylogenetic diversity, and no compositional uniqueness is black, and a pixel with maximal values for  
290 each is white. This additive model conveys both the intensity of the overall risk, but also the nature of the  
291 risk as colors diverge towards combinations of values for three risk components. Out of the possible  
292 combinations, the most risky in terms of rapid diversification and spillover potential is high phylogenetic  
293 diversity and low viral sharing,<sup>64</sup> in that this allows multiple independent host-virus coevolutionary  
294 dynamics to take place in the same location. In the colorimetric space, this corresponds to yellow – because  
295 the HSV space is more amenable to calculations for feature extraction,<sup>65</sup> we measured the risk level by  
296 calculating the angular distance of the hue of each pixel to a reference value of 60 (yellow), and weighted  
297 this risk level by the value component. Specifically, given a pixel with colorimetric coordinates ( $h, s, v$ ), its  
298 ranged weighted risk value is

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

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

### 300 **Viral phyogeography and evolutionary diversification**

301 To next represent phyogeography of betacoronaviruses in bats, we aggregated and analyzed  
302 betacoronavirus sequence data. We used the following query to pull all *Betacoronavirus* sequence data  
303 from the GenBank Nucleotide database except SARS-CoV-2; (“Betacoronavirus”[Organism] OR  
304 betacoronavirus[All Fields]) NOT (“Severe acute respiratory syndrome coronavirus 2”[Organism] OR  
305 sars-cov-2[All Fields]). We added a single representative sequence for SARS-CoV-2 and manually curated  
306 to remove sequences without the RNA-dependent RNA polymerase (RdRp) sequence or that contained  
307 words indicating recombinant or laboratory strains including “patent”, “mutant”, “GFP”, and  
308 “recombinant”. We filtered over-represented taxa including betacoronavirus 1, hCoV-OC43, Middle East  
309 respiratory syndrome coronavirus, Murine hepatitis virus, and hCoV-HKU1. Curated betacoronavirus  
310 RdRp sequences were then aligned using MAFFT<sup>66</sup> v1.4.0 (Algorithm FFT-NS-2, Scoring matrix 200PAM /  
311 k=2, gap open penalty 1.53m offset value 0.123) and a maximum likelihood tree reconstructed in  
312 IQ-TREE<sup>67</sup> v1.6.12 with ModelFinder<sup>68</sup> ultrafast bootstrap approximation<sup>69</sup> with a general time reversible  
313 model with empirical base frequencies and the 5-discrete-rate-category FreeRaye model of nucleotide

314 substitution (GTR+F+R5).

315 We first tested the hypothesis that hotspots of viral diversification would track hotspots of bat  
316 diversification. To do so, we plotted the number of known bat hosts (specifically only those included in the  
317 phylogeny, so there was a 1:1 correspondence between data sources) against the “mean evolutionary  
318 distinctiveness” of the associated viruses. To calculate this, we derived the fair proportions evolutionary  
319 distinctiveness<sup>70</sup> for each of the viruses in the tree, then averaged these at the bat species level, projected  
320 these values onto their geographic distributions, and averaged across every bat found in a given pixel. As  
321 such, this can be thought of as a map of the mean evolutionary distinctiveness of the known viral  
322 community believed to be associated with a particular subset of bats present.

### 323 **Co-distribution of hosts and viral hotspots**

324 Subsequently, we tested the hypothesis that the biogeography of bat betacoronaviruses should track the  
325 biogeography of their hosts. To test this idea, we loosely adapted a method from,<sup>71,72</sup> who proposed a  
326 phylogenetic method for the delineation of animal biogeographic regions. In their original method, a  
327 distance matrix - where each row or column represents a geographic raster’s grid cell, and the dissimilarity  
328 values are the “beta diversity similarity” of their community assemble - undergoes non-metric  
329 multidimensional scaling (NMDS); the first two axes of the NMDS are projected geographically using a  
330 four-color bivariate map. Here, we build on this idea with an entirely novel methodology. First, we  
331 measure the phylogenetic distance between the different viruses in the betacoronaviruses tree by using the  
332 cophenetic function in ape;<sup>73</sup> subsequently, we take a principal components analysis of that distance  
333 matrix (readily interchangeable for NMDS in this case) to project the viral tree into an n-dimensional  
334 space. We then take the first two principal components and, as with the evolutionary distinctiveness  
335 analysis, aggregated these to a mean host value and projected them using a four-color bivariate map.

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Figure 1: 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.

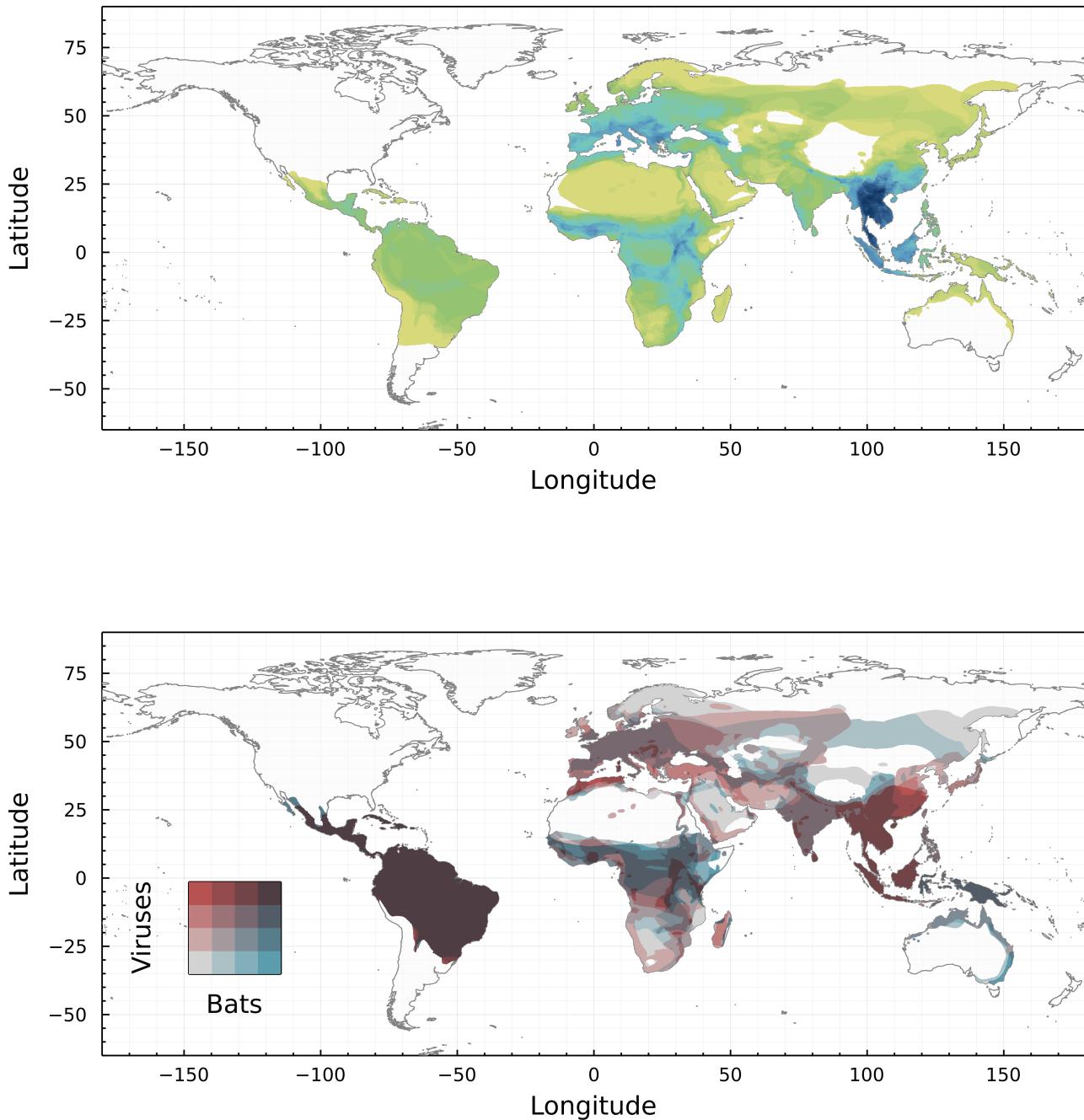


Figure 2: Top panel: relative diversity of known bat hosts of betacoronaviruses. This map shows that the region with the largest number of possible hosts is South-Eastern Asia. Bottom panel: congruence between the evolutionary distinctiveness of the hosts (grey to blue) and the viruses (grey to red).

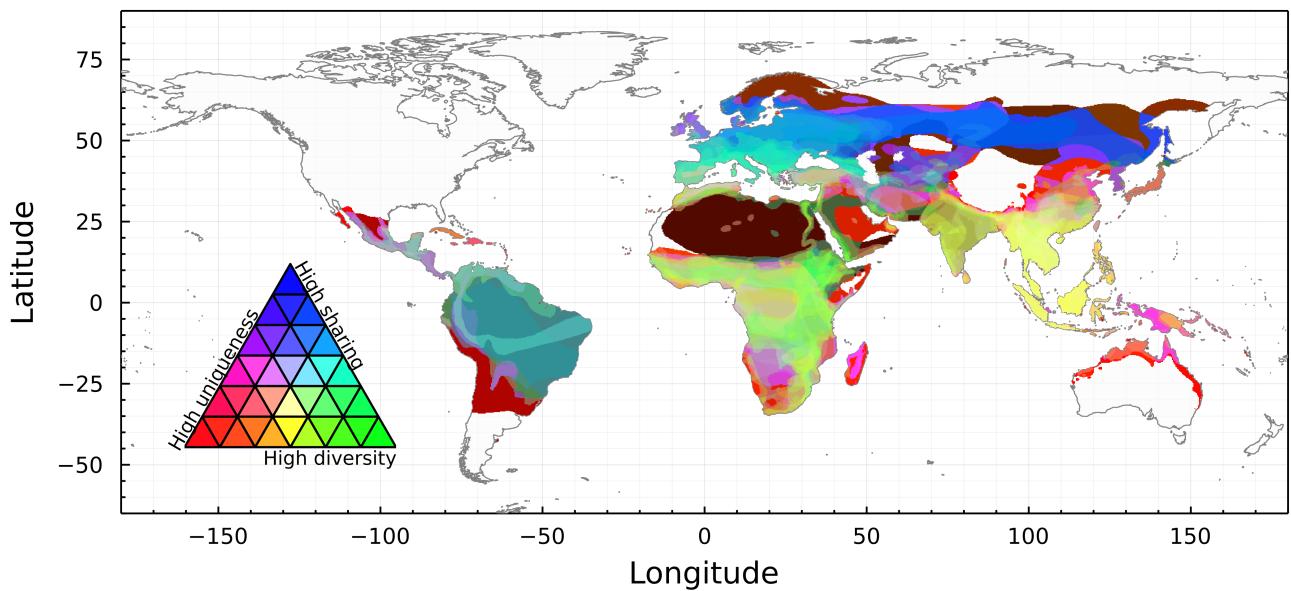


Figure 3: Trivariate additive mapping of the components of risk. Viral sharing runs from yellow (low) to blue (high); host phylogenetic diversity runs from pink (low) to high (green) channel, and compositional uniqueness runs from cyan (low) to red (high). The GMTC suggests that the highest evolutionary potential for emergence exists in unique and diverse host communities with low viral sharing, *i.e.* pixels around yellow.

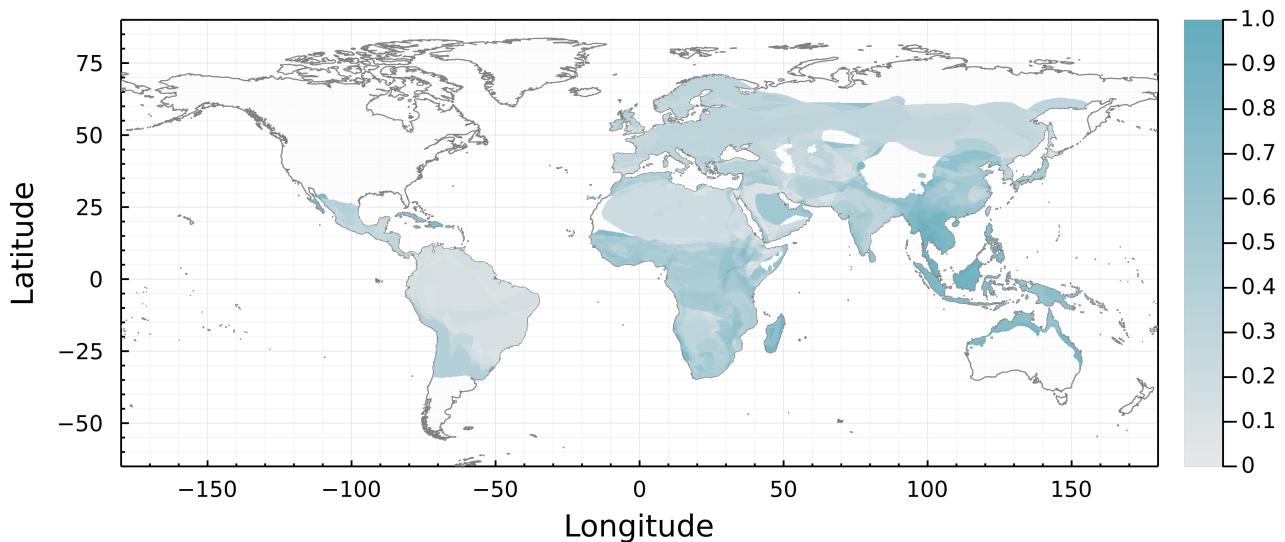


Figure 4: Extraction of a measure of *Betacoronavirus* emergence risk from bat hosts based on the colorimetric space from fig. 3. The risk is a composite measure of the color value and angular distance to the yellow hue, as defined in the methods, ranged in the unit space. Based on these analyses, South-Eastern Asia, Madagascar, the Middle-East, and Africa below the Sahara desert have the highest relative risk of emergence.

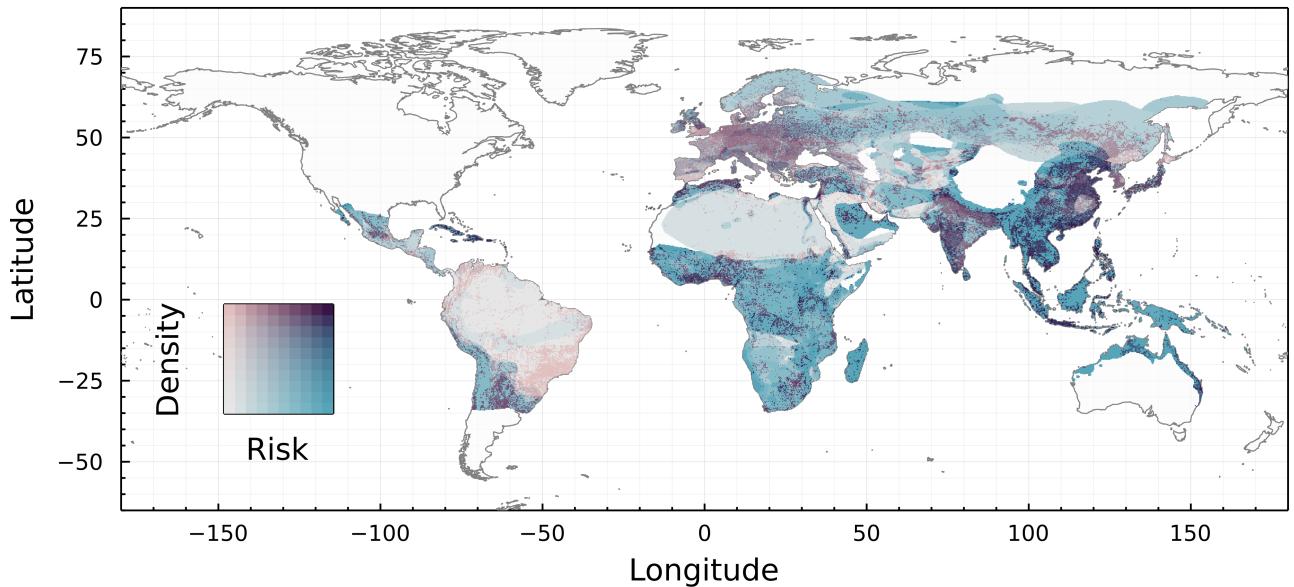


Figure 5: Overlap of the percent of each pixel occupied by urbanized structures, representing the degree of settlement, on the spillover risk map (where the risk comes only from wildlife, and ignores multi-hosts chains of transmissions including non-bats hosts). Darker pixels correspond to more risk, 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 highlights the risk in India, southeast China, and the Arabian peninsula where areas of high to moderate risk overlap with areas of denser population.